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Wstęp do rewizji systematycznej rodziny *Agromyzidae* (*Diptera*) z uwagami na temat wybiórczości tych muchówek

Введение в систематическую ревизию семейства *Agromyzidae* (*Diptera*) с замечаниями по вопросу о выборе этими двукрылыми кормовых растений

Introduction to a Systematic Revision of the Family *Agromyzidae* (*Diptera*) with some Remarks on Host Plant Selection by these Flies

[With 70 text figures]

CONTENTS

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THREE FUNDAMENTAL FEATURES OF NEONTOLOGICAL SYSTEMATICS

Mayr, Linsley and Usinger (1953) defined biological systematics as "the science of classification of organisms". However, the definition is too broad because organisms can be classified in various ways, according to the adopted principle of classification. Among many existing and possible biological classifications there is only one particular kind of classification, called the natural system, which is the subject of systematics as an independent science.

Biological systematics is a science of the natural system of organisms, and its branch, neontological systematics, is a science of the natural system of recent organisms.

The principle of the natural system is not the mere resemblance of organisms but their relationship, that is their common origin. In other words, systematics classifies organisms not so much according to the degree of their resemblance as according to the degree of their relationship.

Idealistic morphology (morphological typology) reduces the aim of systematics to the discrimination of "essential" similarities (homologies) from "non essential" similarities (analogies). The natural system should be based on the principle of a common plan of structure, i. e. on the principle of structure homology, and phylogeny, in turn, should "translate it into the language of the theory of descent" (Remane, 1952). Yet, idealistic morphology is not able to give such a definition of homology, which would not refer to the criterion of common origin. Remane (1952) who, trying to deduce the idea of homology in an empiric way, makes it, in fact, a derivative of the idea of phyletic relationship (cf. Hennig, 1953).

Since the relationship of organisms is the result of their reproduction, the aim of systematics lies in distinguishing the interbreeding organism communities, i. e. species, and moreover, in classifying the species in higher units of the natural system according to the degree of their phyletic relationship.

As a community of actually or potentially interbreeding organisms, practically isolated from other such communities, the species is a real and objective

phenomenon in nature. It is an evolutionary originated form of existence of living beings which reproduce bisexually (Dobzhansky, 1941; Mayr 1942). The species occupies an exceptional position in the taxonomic hierarchy, since it is the only category which can be objectively defined by the criterion of interbreeding (Mayr, 1953). The relationships between the individuals of an amphigonic species are of a reticulate form and, consequently, they are of a different nature than the relationships between the species and their groups, which are presented by the divergent and hierarchic system in the shape of a tree (Remane, 1952). Though the tree also represents the relationships within species of either exclusively vegetative, autogamous or parthenogenetic reproduction, but species of that kind proved to be far more rare than it was thought.

The species is a stage of the evolutionary process, a state of equilibrium in the process, or as it was defined by Hennig (1950), "a state of equilibrium between the evolutional differentiation pressure and the conservative principle of bisexual reproduction". The reality of the species does not mean their strict isolation in time and space. Biological isolation grows gradually and having become established it can be disturbed again. Because of that, incipient species not always can be distinguished from subspecies or even from races, while hybrids of species that are feebly differentiated may appear and then to a certain extent disturb the divergent system (Dobzhansky, 1941; Mayr, 1942, 1953; Hennig, 1950; Remane, 1952).

Species are connected with their ancestral species by a continuous stream of generations, nevertheless, the degree of reality of species is higher than that of other taxa[1]. Some deviations exist here similarly as deviations from the intergrity of individuals or cells, but the species remains like the individual or the cell, the essential biological unit (Huxley, 1942). Thus, the dynamic conception of an interbreeding community does not justify the subjectivistic definition of the taxonomic species. The taxonomic species exists objectively as a community of actually or potentially interbreeding organisms, to which the individual designated as a standard of the nominal species (type-specimen, type) belonged.

The higher, supraspecific taxonomic units are of merely "relative reality". They exist in fact as monophyletic species groups, but their rank in the systematic hierarchy cannot be defined objectively (Mayr, 1953). The criterion of the period of duration (or time of origin) proposed by Hennig (1950) cannot be accepted on account of the inequal tempo of evolution in various groups and in different periods of time. The rank of a higher taxon is fixed conventionally, according to its differentiation from other groups and inner differentiation degrees and to the number of its representatives.

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[1] Transspecific transformations show probably an accelerated tempo, although they may be, as a rule, gradual within the limits of the speciation period.

Every higher taxonomic unit has a single species as its ancestor, each unit originating through speciation. Thus, the species is the essential element of the natural system, and the problem of speciation stands as the chief problem of systematics. Phylogenesis consists of a number of repeated speciations (Hennig, 1957).

The natural system representing the mutual relationship of the species must be consistently phylogenetic. It is in accordance with the genealogical tree displaying the monophyletic and divergent evolution of the organic world (Haeckel, 1866). Since the tree is monobasic and ramified as a rule dichotomously, the natural system must be hierarchic allowing only vertical divisions into monophyletic groups. All horizontal divisions into polyphyletic groups, caused by parallel or convergent evolution, are artificial and cannot be accepted as natural taxonomic divisions.

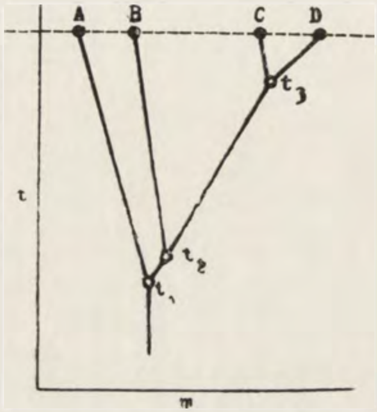


Fig. 1. Simple way of speciation (after Hennig, 1953, modified).

The degree of phyletic relationship of descendent species is objectively defined only by the number of ramifications of the genealogical tree, dividing the descendent species from their common ancestor [Fig. 1]. "A species B is more closely related to a species C than to any other species A then and only then when it has at least one common ancestral species with the species C, which at the same time is not an ancestral species of A" (Hennig, 1953). The quoted definition of phylogenetic relationship fulfils the logical requirements of the hierarchic system which reflects the objective relations between species. Classifications based on resemblance or relationship understood otherwise are subjective and have no sufficient logical grounds (Hennig, 1957).

Deviations from the divergent (dichotomous) system, in which every ancestral species splits into two descendents, are treated here as borderline cases which in principle do not contradict the above definition of the phylogenetic relationship. These deviations are as follows: polytomy, digression, succession and bastardization. Polytomy, i. e. radiation [Fig. 2a] consists

probably, in fact, in the presence of minimal distances between the neighbouring ramification points of the genealogical tree or in a considerable overlapping of the speciation periods which follow one upon the other. Digression of a descendent species from its ancestor which subsequently continues to exist together with the descendent [Fig. 2b] can also be interpreted as a minimal deviation of one of the two descendent species from its ancestral species (cf. HENNIG, 1953). An extreme variety of digression would be represented by the iterative origin of species [Fig. 2c], i. e. an independent digression, from the same ancestral species, at different times, of descendent species very similar to each other but directly unrelated. This is considered to be a particular case of heterochronic parallelism. Succession [Fig. 2d] consists in the gradual transformation of an ancestral species into one descendent species, i. e. without splitting or digression. This mode of species-formation is probably more rare than it is generally assumed according to paleontological data. More often we are dealing rather with a digression of descendent species and a relatively quick extinction of the ancestral species. Finally, bastardization, i. e. interspecific hybridization being a particular case of convergence widely conceived (cf. HUXLEY, 1942) consists in the origin of hybrid (polyphyletic) species either by the repeated fusion of two previously separated species [Fig. 2e), or by cross-breeding of only certain individuals or populations of two species [Fig. 2f] or by the joining of certain individuals or populations of one species to another [Fig. 2g]. Interspecific cross-breedings are fairly common in the plant kingdom and play there a more considerable role in evolution (STEBBINS, 1950). Bastardization repeated in various combinations results in the so-called reticulate evolution (HUXLEY, 1942) resembling the evolution of races within a single species. In the evolution of animals, however, bastardization seems to be scarcely of any importance. Interbreeding communities that are not completely isolated in nature may be regarded here as incipient species bordering on the stage of races.

Admitting certain cases of polyphyletism of species, we reject, however, the polyphyletism of higher taxonomic units since, in fact, they always originate from single species (though sometimes from polyphyletic species). In cases when we notice that the development from genus to genus, from family to family, etc., proceeds along many parallel lines (SCHINDEWOLF, SOBOLEV), this can be explained either by the existing classification being artificial or by the fact that the principle of the natural system is not respected. "Cutting off and binding" of unconnected though very close and parallel branches of the genealogical tree of species means establishing of polyphyletic groups as well as preference of morphological resemblance to relationship. Besides, phylogenetic parallelism never affects all characters of the organisms, but merely some of them. Just because of the different intensity of this parallelism horizontal divisions are always more or less arbitrary. Thus, they can neither be respected nor acknowledged as taxonomic divisions (as HUX-

LEY, 1942, or MAYR, 1953, insist). Conversely, they should be abolished as species relationships are better known (cf. REMANE, 1952). Parallel evolution is an objective and widespread phenomenon, yet horizontal divisions do not reflect the phenomenon but, on the contrary, they confuse it as well as obscure the natural relationship of the species. If too scarce an attention has been

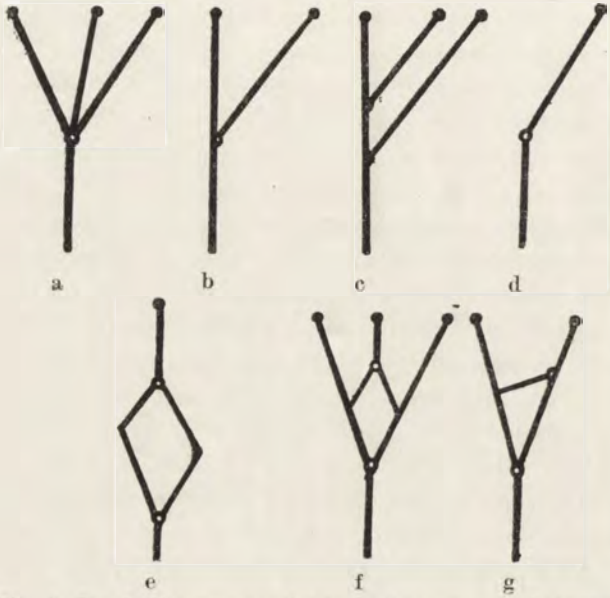


Fig. 2. Borderline cases of speciation: a — polytomy (radiation), b — digression, c — iterative species-formation, d — succession, e, f, g — bastardization.

paid to the universality of parallelisms so far, it is due to the confusion of vertical and horizontal divisions, which the existing taxonomic arrangement presents.

A natural system which should display the whole of the genealogical tree of the organic world is the common aim of both paleontology and neontology. Such a ,,three-dimensional" arrangement results as a combination of "two-dimensional" arrangements which give horizontal cross-sections of the genealogical tree, at particular time levels. The highest of these cross-sections, the one which is reached by the tips of all the living branches of the tree, corresponds to the natural system of the recent organisms, constructed by neontological systematics. We project the tree upon a plain and then, by shifting such a plain cross-section of the tree to a straight line we obtain a linear system [cf. Fig. 1].

To build such a linear system of recent species, neontological systematics must therefore reconstruct their genealogical tree starting back from the tips of its living branches. Up to a certain extent, the principle of the "three-

fold genealogical parallel" (dreifache genealogische Parallele; HAECKEL, 1866) suggested the method by which the task could be realized, and the principle of "parallel between phyletic (paleontological) and systematic (specific) developments" in particular, the latter being understood by HAECKEL as the natural system of recent organisms. Owing to the irregular tempo of evolution, the various side branches of the genealogical tree deviate from the ancestral branches not only in different directions but also to a different extent. Thus, the natural system of recent animals and plants provides us with a partial picture of ways and stages of their phylogenesis.

HENNIG (1950) recently defined this regularity by means of the so-called deviation rule (Deviationsregel). This rule points out that while an ancestral species splits into two descendents, one of them either does not deviate at all or deviates from the ancestral species less than the other. The same rule refers to higher systematic groups. HENNIG calls features or forms corresponding to ancestral (original) ones — plesiomorphous (plesiomorph), while changed and deviated — apomorphous (apomorph). These terms substitute successfully the ambigous ones used until now, such as "primitive" or "conservative" and "specialized" or "progressive".

Starting from the deviation rule, HENNIG precised certain kinds of homology for the purposes of phylogenetic systematics. As a proof of a close relationship of species (or their monophyletic groups) there is only one kind of homology called synapomorphy (Synapomorphie), i. e. resemblance in apomorphous features. The kind of homology called symplesiomorphy (Symplesiomorphie), i. e. resemblance in plesiomorphuos features, does not prove a close relationship. Furthermore, homology can be the result of convergence[1] when species (or groups) are similar in their autapomorphies (Autapomorphien), i. e. apomorphous features which their ancestors did not bear. In reversible evolution of some features, homoiologies can seem to be synapomorphies or symplesiomorphies (cf. HENNIG, 1953).

If the phylogenetic relationship is the only objective principle of the natural system of species, phylogeny cannot be a separate science but is an integral part of systematics, one of its branches. This branch performs a more nomothetic research function concerned with the relationship and origin of species and their groups. A more idiographic function concerned with distinguishing and describing of species and their groups is the aim of taxonomy. This term, applied first by DE CANDOLLE (1813), primarily meant "the theory of plant classification" but now it is widely used in the meaning which we ascribe here to it.

The phylogenetic basis of taxonomy, recently postulated mainly by HENNIG (1950, 1953, 1957), has not been fully acknowledged by the founders of the

[1] In the broader meaning of both terms. In our opinion this is rather homoiology (parallelism).

so-called new systematics: Huxley (1940, 1942), Dobzhansky (1941) and Mayr (1942, 1953). They, like Wettstein (1933), admit deviations from the consistently phylogenetic system which would be an "unattainable ideal" and this even "if all the facts of phylogeny would be known"; they admit these deviations with regard to the need of compromise with practical postulates of the clearness of the system. In their opinion, the degree of relationship can be designated not only according to the number of ramifications dividing the branches of the genealogical tree but also according to the distances between the ramifications and according to the declinations of the branch tips. If the horizontal divisions may be more "useful" than vertical ones they should not be eliminated, all the more as they became rooted in the minds of biologists. This tendency to make taxonomy independent from phylogeny is connected with depreciation of the influence the evolutionary theory has been exerting upon the progress of systematics.

It is sometimes difficult to realize a consistently phylogenetic system even in principle (particularly in the case of "reticulate evolution") but we regard all the deliberate and avoidable deviations from the system as contradictory to the aim of systematics as a science.

The phylogenetic relationship, which can be defined in time, is the only objective criterion of the natural system of species. References to the criteria of resemblance make systematics a more or less arbitrary subject. Now, if we admit this only objective criterion as the base of taxonomy then, in order to make the nature anwer the question asked, we must use it uniformly and consistently. A classification, even partly artificial, obscures the picture of evolution and distorts the knowledge of its regularities — nor does it reflect the objective state of things which was formed as a result of this historical process. Besides, an artificial system seems to be more practical and clear than the natural one only when we approach the organisms in a superficial and one-sided way. As we apply more many-sided investigations, all the incongruities of the artificial system will immediately make their appearance, such as the incongruity of imaginal and larval systems, the lack of geographic and ecological replacement of species and groups allegedly related, unexpected vast differences in sexual organs, full incongruity of host and parasite systems etc. Often we do not even realize how many false concepts in various biological disciplines were caused by artificial classifications.

Existing taxonomic arrangements were established not only by various authors but also according to various principles, at times according to this or that resemblance of organisms, and at other times according to their relationship, however, understood in different ways, either as synapomorphy or as symplesiomorphy or even as homoiology. Consequently they present a confusion of vertical and horizontal divisions, of monophyletic, typological and even obviously polyphyletic groups. Therefore, we do not share fully the optimism of Dobzhansky (1941) and Mayr (1942), when they state that "the classi-

fication now adopted is not an arbitrary but a natural one reflecting the objective state of things" and that "the subdivisions of the animal and plant kingdoms established by LINNAEUS are, with few exceptions, retained in the modern classification". We can agree with these statements only as far as they oppose some attempts to disregard totally and to undermine present day systematics or oppose, at any rate, a too sceptical approach towards its results. In post-LINNAEAN times systematics advanced considerably, particularly owing to the success of the evolutionary theory. But to realize how far away are present classifications from the natural classification it is enough to notice the fact that two-thirds of animal species are insects, the majority of which is very slightly and superficially known even as far as adult morphology is concerned, not to mention ecology and development cycle. Our pessimism contains yet a certain dose of optimism which enables us to believe that systematics has still great prospects lying ahead.

Systematics as every science, develops gradually and approaches truths through series o,f hypotheses. In fact, we are never provided with direct proof of the relationship and origin of species and all our phylogenetic views are of a hypothetic value, and were developed by comparison and inference. Thus, while speaking of deviations from the natural system as undesirable, it is only the principle of our procedure in science and the objective we aim at.

Defining phylogeny as a more nomothetic and speculative branch of systematics, at the same time, we do not consider taxonomy as a branch purely idiographic and empiric. Similarly as the origin of species, which determines their natural classification, is never directly recognizable, so the community of interbreeding organisms cannot be grasped as a whole directly in nature. Both criteria are, however, the only objective ones and systematics would be unable to exist as a science without accepting them. Thus, taxonomy also recognizes the objective reality in an indirect way, by means of comparison and inference, and the vast majority of its statements is of a hypothetic value.

The base for conclusions concerning relationship of organisms and species is constituted by their resemblances and differences.

Reproductive isolation facilitates divergency of all characters, increasing constantly as the isolation period continues. Therefore, the objective discontinuities of organism differentiation are generally a sufficient base for their natural classification and guarantee a considerable degree of likelihood of systematic diagnoses (DOBZHANSKY, 1941; MAYR, 1953). Yet the processes of divergency of particular characters are not strictly correlated with each other, and in various organisms they are correlated in a different way. This mosaic pattern of evolution consists in the unequal tempo of evolution of particular characters, of various organism groups and in different periods of time, specialization crossing, reversibility of evolution of particular characters, convergence and parallelism, bastardization, and certain discontinuity of intraspecific variability (polymorphism). Various characters are of different

value for systematics but a constant gradation of their value does not exist, moreover none of the characters has any universal indication value which would replace objective criteria, i. e. the criterion of interbreeding and that of phyletic relationship. Thus systematic diagnosis demands such an evaluation of characters which would approximate it to a diagnosis based on objective criteria. The method of such an analysis and evaluation of characters is the "mutual elucidation method" (Methode der wechselseitigen Erhellung; Hennig, 1950), based on many-sided approach towards organisms and on mutual supplementing of induction with deduction.

The natural classification of living beings demands a many-sided investigation of them. Differences between organisms and between species appear in many aspects, not only in morphological features but also in physiological, biochemical, ecological, ethological, geographic etc. All these differences, as originated in the course of time, refer to the relationship and enable us to get an opinion concerning it (Hennig, 1950, 1953). The more many-sided and complex our approach towards organisms, the more effectively we can apply "the mutual elucidation method" — hence the higher degree of likelihood of our systematic diagnoses.

The representatives of the so-called new systematics, for instance Mayr, Linsley and Usinger (1953) postulate it, in fact, to be many-sided and biologized as opposed to the superficial and narrowly morphological old systematics. However, they do not emphasize enough the fact that the aim of this biologization is not only the better distinguishing of species but also a profound study on their phyletic relationship. By not requiring a consistently phylogenetic system they do not pay enough attention to macrosystematics. They maintain that the highest stage of scientific neontological systematics — "the stage of studies on evolution" — consists in intraspecific systematics which borders on genetics, in quantitative studies on population. All the development of evolutionary studies denies, however, such a restriction of the idea of these studies. As far as biometric methods are concerned, esteeming their importance, we would only like to stress that the quantitative analysis of chosen structural characters should not precede a many-sided qualitative analysis considering biotic characters too.

One-sided systematic diagnoses as far as they are not caused by a subjectivistic attitude towards systematics, express an exaggerated confidence in the law of biological correlation. Since this law, however, as other biological laws, has a limited range only, our diagnoses are also governed by a "law of minimum". The systematic diagnosis needs a certain minimum of information concerning external and internal morphology of the adult, development cycle, ecological niche and geographic distribution. A very detailed study of the external morphology (or skeleton parts), even including biometric analysis, will not fully substitute the study on certain internal structures (or soft parts) and the latter, in turn, will not fully substitute the study on ontogeny, eco-

logy, ethology and geographic distribution, as much as a detailed study on the development cycle and ecological niche will not be able, of course, to substitute the study of adult morphology of both sexes. It is true that the existence of "physiological species" structurally completely undifferentiated was not proved yet, but we know many examples of extremely scarce and indistinct differentiation of structure of species having clearly distinct physiology, ecology and ethology (Thorpe, 1940; Mayr, 1942, 1953). The interspecific morphological differences are neither larger nor always of different nature than the intraspecific differences, since sibling species (Mayr, 1942) and polymorphism exist side by side. Thus, the morphological (typological) concept of the species (morphospecies) was substituted by the biological concept of interbreeding community (biospecies).

Phylogenetic relationship cannot be reduced also to simple morphological typology, to some common plan of structure, or to some maximum correlation of structural characters. Not only idealistic morphology but even phylogenetic morphology comprising comparative anatomy, embriology and paleontology would not be, all alone, a sufficient basis for phylogenetic systematics. Holomorphological method should be supplemented with chorological analysis revealing the geographic and ecological replacement of closely related species as well as their monophyletic groups (Hennig, 1950).

The possibility of a many-sided approach to living organisms is a marked advantage of neontological systematics as compared with paleontology. This is compensated in paleontology by the time factor which is connected with the stratigraphic arrangement of fossil organic remains and in general with the possibility of stating their age. Yet, paleontology also does not explore evolution and phylogenesis in a direct way, but does it indirectly by means of comparison and conclusion (Sewertzoff, 1931; Hennig, 1950; Remane, 1952). If there is a common opinion that paleontology is a more evolutionary science than neontology, it is probably because the latter has not played its trump sufficiently.

We have tried to shaw that neontological systematics has three fundamental, mutually conditioned features: it is phylogenetic, objective and many-sided.

Systematics is phylogenetic (evolutionary) because it regards species as stages and states of equilibrium of the evolutionary process and because it classifies them into a hierarchic system (in monophyletic groups) according to the criterion of phylogenetic relationship, i. e. common origin, and by this it contributes to the reconstruction of the genealogical tree of the organic world.

Systematics is objective because it distinguishes communities of actually or potentially interbreeding organisms (species) really existing in nature and because it arranges them into monophyletic groups, according to the objective criterion of phyletic relationship which can be determined in terms of time.

Systematics is many-sided (complex) because it recognizes interbreeding communities and their relationship not directly but by means of the method of mutual elucidation which is based on the analysis of all kinds of resemblances and differences between organisms, i. e. on results obtained in all other biological sciences.

The whole of our knowledge of the organic world has been compared to a layer-cake, vertical cross-sections of which are formed by systematics, while the horizontal strata belong to other biological sciences. This metaphor very well shows the exceptional function of systematics with regard to other sciences. Being a repeated cross-section of the biological sciences, and at the same time, an independent science, systematics to an equal extent makes use of all these sciences as well as serves them with results of its investigations. In this respect, systematics would be treated as a general classification of all the classifications made by other biological sciences (Hennig, 1950).

INTRODUCTION TO A SYSTEMATIC REVISION OF THE FAMILY *AGROMYZIDAE*

It is of essential importance for a natural classification of animals — apart from a detailed knowledge of the morphology of the adult — to know their development cycles and their ecological niches as well. There is a better chance of achieving this in groups of organisms ecologically specialized, particularly of host specialized parasites. As parasitological systematics deals with the mutual relations of two closely connected groups of organisms, it has at its disposal certain additional methods and criteria, such as host-parasite discrimination method, parasitogenic rules etc.

As both the host and the parasite may belong to one of the two kingdoms of the organic world, four types of parasitic relations may be distinguished as follows: 1) animal parasite — animal (or human) host, 2) plant (or bacterian) parasite — animal (or human) host, 3) animal parasite — plant host, 4) plant (or bacterian) parasite — plant host. Modern parasitology, as a zoological science, is practically limited to the study of only one (the first one) of the four types of parasitism mentioned. In practice parasitology leaves aside not only all parasitic plants (bacteria included), but also phytophagous animals that show a constant space connection with their host plants, larger than themselves, and have a way of life which is parasitism in the general biological sense of the term. At the same time, parasitology includes investigations on animals of a disputable parasitic character. It takes into account not only blood-sucking animals but also the so-called parasitoid insect larvae, e. g. of *Terebrantia* or of *Tachinoidea*, which may be called internal predators rather than parasites (cf. Allee, 1949), if they are of about the same size as their

non-specific "hosts" or rather their prey which they ultimately kill. As both systematic (taxonomic) and biotic (ecological) criteria delimit the scope of modern parasitology, it is sometimes referred to as zooparasitology, whereas the field of study on both animal and plant parasites of plants, not yet developed as a distinct science, is called phytoparasitology. The author suggests here the term "zoophytoparasitology" to denote a science of parasitic relations between animals as parasites and plants as hosts.

One of the typical groups of zoophytoparasites are leaf mining insects (leaf miners), the larvae of which feed inside living green plant tissues, leaving characteristic feeding patterns called mines. The knowledge of the ecology of these larvae was developed mainly due to the investigations of Erich Martin Hering, conducted about 40 years, into a separate branch of entomology called minology (hyponomology) which should be, at the same time, a branch of zoophytoparasitology. The systematics of leaf miners, the latter being specialized temporary endoparasites of plants, could be of a more "parasitological" character than the systematics of some other groups of animal parasites. This is the result of the following circumstances:

1. Active choice of host plants by mining insects and host plant specificity reduce to a minimum the probability of an occasional occurrence of the parasite on a non-specific host.
2. Topospecificity of the parasite is manifested by a specific feeding pattern of the larva inside a defined plant organ and tissue.
3. As the endophagous larva is not able to migrate from plant to plant[1], its space connection with a plant always depends on feeding, on a specific host-parasite relation.
4. It is easy to collect larvae and it is possible to rear adults from larvae and thus to examine all the development stages important in taxonomy.
5. Due to the immobility of the host plants it is easier to investigate the influence of the secondary environment factors.

The above circumstances make possible some confrontation of morphological and ecological data at the various stages of the ontogeny of the parasite, some use of host-parasite discrimination method and — to a certain extent — some mutual verification of both the host and parasite systems.

A particularly narrow specificity of the host-parasite relation is characteristic for most representatives of the family *Agromyzidae*. This family is one of the main groups of leaf mining insects though some of its members preserved different types of endophagy. For a systematist these dipterous insects have an advantage over other groups of miners as their males show a very complex structure of their copulatory apparatus, peculiar to the particular species. This facilitates the recognition of interspecific structural differences and phylogenetic relationship as well. Yet the investigations carried out so far have

[1] Moths of the family *Coleophoridae* make a remarkable exception.

not made use of it, and the genitalia have been known and described (or only illustrated) but for a small number of *Agromyzidae* with no conclusions having been drawn. That is why the classification within the family, in spite of the larval ecology and morphology being known, was decidedly artificial.

The family *Agromyzidae* is considered to be one of the most difficult and, at the same time, most carefully studied groups among dipterous insects and — may be with the exception of the *Drosophilidae* — the best known group of minute flies. Considerable progress in the study of the family has been noted since the twenties of this century[1]. At that time Friedrich Hendel (Austria), J. C. H. de Meijere (Netherlands) and Erich Martin Hering (Germany) simultaneously started separate investigations on the adults, larvae and mines. The result of their collaboration as well as that of the contributions of other entomologists was a detailed monograph of the family written by Hendel (1931—1936); it contains descriptions or redescriptions of 350 Palaearctic species. The descriptions of the larvae by de Meijere were gradually apearing in the years 1925—1950. The results of the studies by Hering are given mainly in his works: "Die Ökologie der blattminierenden Insektenlarven" (1926), "*Agromyzidae*" (1927), "Minenstudien" (a set of papers published in the years 1920—1944), "Die Blattminen Mittel- und Nordeuropas einschliesslich Englands" (1935—1937). After the death of Hendel (1936) and later after that of de Meijere (1947) Hering continued his studies on the *Agromyzidae* in all the three directions; he described many mines, larvae and new species. In 1951 his excellent synthetic work "Biology of the Leaf Miners" was published, and in 1957 his large "Bestimmungstabellen der Blattminen von Europa" (extended to three volumes). In the meantime some new specialists appeared: Nils Rydén (Sweden) published since 1929, Kenneth A. Spencer (Great Britain) — since 1953, G. C. D. Griffiths (Great Britain) — since 1954, J. T Nowakowski (Poland) — since 1954, M. Sasakawa (Japan) — since 1953 and M. Kuroda (Japan) — since 1956. From among entomologists who were incidentally interested in studying the *Agromyzidae* after 1930, the most important contributions were made by the Italian investigators F. Venturi and M. Ciampolini. The valuable papers of H. Buhr and F. Groschke (Germany), and E. Kangas (Finland) were also of considerable importance. G. Enderlein (Germany) suggested in 1936 a new generic division of the family but no one followed him. Compiled keys to the *Agromyzidae* are published in the works of A. Stackelberg (USRR, 1933) and E. Séguy (France, 1943). W. Hennig (Germany) gave notes and comments on all papers dealing with the larvae (1952) and later with pests (1953b). Some minor taxonomic and faunistic papers, on mines, or dealing with plant protection had been published after 1930 by: H. Franz (Austria), v. d. Bruel, A. Collart (Belgium), B. Kvičala, E. B. Rohdendorf-Holmanova, B. Starý, A. Vimmer (Czechoslo-

[1] Earlier investigations are reported by Frick (1952).

vakia), H. Soenderup (Denmark), S. M. Hammad, A. Maher (Egypt), R. Frey (Finland), J. d'Aguilar, L. Mésnil, R. Régnier, E. Séguy, R. Séllier (France), K. Berger, K. Busse, W. Eichler, J. Haase, O. Karl, O. Kröber, A. Ludwig, M. Lüdicke, G. Nietzke, E. Schimitschek, J. Seidel, H. Starke, G. Voigt (Germany), P. Allen, H. Barnes, M. Cohen, M. Niblett, L. Parmenter, A. M. Russel, E. R. Speyer (Great Britain), P. Suranyi (Hungary), E. Rivnay and S. Zimmermann (Israel), G. Della Beffa, G. M. Martelli, A. Melis (Italy), S. Kato, K. Koizumi, S. Kuwayama and Y. Nishijima, M. Tsujita (Japan), M. Beiger, M. Nunberg, J. W. Ruszkowski (Poland), E. Dobreanu (Rumania), B. J. Bielskij, B. B. Rohdendorf, A. A. Stackelberg (USRR). Continued interest shown in the family *Agromyzidae* is proved by the fact that up till now there are over 750 species of these flies known in the Palaearctic Region, thus, more than 400 species have been described or redescribed since the publication of Hendel's monograph.

More recent investigations of the Nearctic fauna have been conducted mainly by S. W. Frost and K. E. Frick who published in 1952 a generic revision of the family *Agromyzidae* with a catalogue of about 250 American species. A synopsis of the Ethiopian *Agromyzidae* comprising 128 species was recently given by Spencer (1959). The knowledge of the fauna of other regions is so far very scanty and fragmentary.

The work of Hendel (1931—1936) provided a broad basis for further investigations. These have given a great deal of new and valuable data but have partly failed to arrange and elucidate these data as they had to omit for the time being the most difficult and most essential task, i. e. examining the genital apparatus. Inadequate knowledge of the morphology had its negative influence on the konwledge of the ecology and very often has made the distinction and identification of species impossible and their natural classification still more so, consequently, the taxonomical arrangement was remaining artificial and obscure. Hendel's key which has been repeatedly supplemented is of no use for an exact identification of species from many a group, and not once taxonomic diagnoses that had been based upon general external morphology of adults were discovered to be erroneous.

The first thorough attempt to give a general description of the male terminalia in the *Agromyzidae* was done by Frick (1952), yet he failed to give a "generic revision". De Meijere (1950) had already to raise some doubts concerning Hendel's generic division of the family as he was unable to find any sufficient basis for it in the larval morphology. Hennig (1952) noticed at once that this division does not present any clear picture. Thus, it was quite surprising that all the large genera of the *Agromyzidae*, differing only in single minute external features, had been confirmed by their genitalic morphology by Frick. When investigating the male genitalia, however, it is seen from the keys and descriptions provided in the "generic revision" that its author has not examined these organs in all or most species of the particular genera but

took into condsideration only a few species chosen as their representatives.

In order to arrange and elucidate the large body of accumulated data as well as to open a broader outlook for future investigations, it seems necessary first to concentrate on a detailed morphology of the genital apparatus. Already the existing knowledge of both larval morphology and ecology together with a more detailed and profound knowledge of the morphology of the adults will make not only adequate distinction and identification of species possible but will reveal their phyletic relationship and thus contribute to a natural system. The latter when compared with the system of host plants, their ecology and geographic distribution, will provide at least a partial knowledge of the pathways which specializing evolution has been and still is following within this group of phytophagous insects. All efforts to study the very complex and differentiated genital apparatus will prove as worthwhile as in the case of the rearing method.

In this situation the author commenced to contribute to a revision of the family *Agromyzidae*. The general introduction given here is dealing mainly with the European fauna and is based upon literature and the following material:

— 2489 specimens of adults belonging to 346 species, of which 1383 specimens have been reared in the laboratory and 1106 captured in the field,
— microscopic slides of the male genitalia of 644 specimens belonging to 280 species,
— about 2500 specimens of puparia,
— microscopic slides of about 700 specimens of larvae,
— about 10000 samples of leaf mines.

This material belongs to the following collections:

— the collection of the author (imagines reared or captured, puparia, larvae, mines) mainly from the Kampinos-Forest near Warszawa and also from other regions of Poland, brought together in the years 1949—1958, belonging to the Institute of Zoology of the Polish Academy of Sciences in Warszawa,
— the collection of O. Karl (imagines reared or captured, puparia) from Polish Pomerania, district Słupsk, made in the years 1924—1935, belonging to the same Institute,
— a part of the collection of F. Hendel (imagines reared or captured, puparia), mainly from Austria and Germany, made in the XIX and XX century, belonging to the Naturhistorisches Museum in Wien,
— the collections of A. Waga, W. Grzegorzek and K. Bobek (imagines captured) from the former Galicia, made in the XIX century, belonging to the Branch in Kraków of the Institute of Zoology of the Polish Academy of Sciences,
— the collection of M. Nowicki (imagines captured) from the former Galicia, made in the XIX century, belonging to the Departament of Zoology of the University in Kraków,
— specimens (imagines reared, puparia, larvae, mines) from Prof. Dr. E. M. Hering's collection, mainly from Germany, made in the years 1921—1955,
— specimens (imagines reared, puparia) from K. A. Spencer's collection from England, made in the years 1954—1956.

Significance of some Aspects of the Investigations

The General External Morphology of the Adult

The monotony of the external appearance of the adults combined with a considerable number of species is characteristic for the family *Agromyzidae*. It is no wonder that systematics based on external adult morphology cannot free itself from ever increasing difficulties. Practice proves doubtlessly that neither the existing differential diagnoses nor keys can be used as a basis for an exact distinguishing and identifying of many "allied" species. It is generally known that in many groups no identification of species can be made without using the rearing method, "the more so if one is not a specialist". That is to say, some external characters of the adults, considered as of taxonomic value, show a loose correlation with those of the larvae and mines. This applies particularly to wing venation, chaetotaxy and coloration. Scores of examples may be quoted of the negligible taxonomic value of such features as costal ratio, the degree of curvature of the radial veins, the ratio of the sections of m_{3+4}, range of *oc*, length ratio of the anterior *ors* to the posterior one, distance ratio of *or*, the number of *ori*, the number of peristomal hairs, the number of *ia* behind the transverse suture of the mesonotum, the number of rows of *acr*, their range in relation to *dc*, the lenght ratio of *acr* to *dc*, the distance ratio of *dc*, the position of *prs* with regard to the transverse suture of the mesonotum, *i. pa*: *e. pa* ratio, number of hairs on the callus humeralis and on the mesopleura, coloration of the angles of the vertex (Scheitelecken), the degree of dullness of the mesonotum, shape and size of the dark spots on the mesopleura, presence of a yellow edge on the upper margin of the sternopleura, color shade of the tarsi and tibiae etc. In spite of the fact that not only these single features but also their combinations are often not reliable, they are still used for diagnostic purposes in describing new species as well as in keys for identification. When the rearing method is used, the ecology of the larva is a starting point for a taxonomic diagnosis, nevertheless, certain traditions and practical purposes demand that the species diagnosis be based on the external morphology of the adult. Consequently, the authors of descriptions look for an adequate "morphospecies" for every "biospecies". Much of the external characters, to which some taxonomic value is attributed, have though not identical, but still overlapping variability ranges. Thus differences that seem to be striking in a small material fail to be so when dealing with abundant series.

The difficulties quoted above indicate the frequent occurence of dual-, crypto-, gemino-, or sibling species. This idea recently precised by Mayr (1942, 1953) is the result of the biological approach to the species, which assumes that divergency of morphological characters — of the external ones at least — may not keep pace with divergency of other features. According to Mayr, sibling species are closely related sympatric species with minimal and imperceptible or inconstant structural differentiation but with a quite different

ecology, physiology or ethology. More clearly defined and more constant morphological differences may either occur in the earlier developmental stages or may be concealed and brought to light only after a detailed examination of some peculiar structures as sense organs or the genitalia.

Taxonomists who exclude the posibility of absence of constant external differences between "good" species would be inclined to explain the difficulties mentioned above as due to insufficient accuracy of descriptions, illustrations and keys, the small size of specimens, poor discernability of some details, bad state of preservation etc. However, every specialist using the rearing method may convince himself that these negative factors are of a secondary importance and even their careful elimination would not help very much. The widespread distribution of sibling species among the *Agromyzidae* is not surprising at all as the species of that kind occur all over the animal kingdom, being especially common among the *Diptera* (Mayr, 1942, 1953).

Even if the lack of any constant external differences between sibling species is not an absolutely objective phenomenon, it is in practice an intersubjective phenomenon. Experience has shown so far that it is impossible to grasp and express these differences — at least in a material of dead specimens of various age and method of conservation — and, consequently, they are often useless for taxonomy based on superficial morphological studies. In the case of some difficult groups many quite desperate attempts have been made to distinguish species according to their external features but they have all failed[1]. Exact biometric methods could help taxonomy but only to a small extent, quite out of proportion to the amount of time and effort required to apply them.

We doubt if the help of biometry can be efficient here, chiefly because lack of constant and perceptible external differences is noticed not only between sibling species but also between species that according to their genital apparatus as well as other characters must be placed far from one another in the natural system. Hering (1939) differentiated such species among the *Lepidoptera* and defined them as "pseudo-Dualspecies"; by analogy we shall use the term "pseudo-sibling species". The so-called "difficult" species groups generally consist of a larger number of sibling species and pseudo-sibling species [cf. pp. 93, 94 and Fig. 8—9]. From mere external morphology we cannot know when the resemblance of species is due to the general low degree of their divergency and when it is the result of some far advanced convergence (more exactly speaking: parallelism or reversibility of evolution of certain characters) and when it results from an unequal tempo of evolution of various features. Parallel reduction of wing venation and that of bristles makes it impossible to base the natural system only on the external characters of the adults (cf. pp. 116—123).

Taxonomists who recognize only a "relative reality" of the species, i. e. who do not trust it is likely to distinguish the species from a subspecies or

[1] Thus e. g. the latest key to the subgenus *Dizygomyza* Hend., s. str. (Groschke, 1957) is little better than the earlier ones.

a race, think that for taxonomic purposes species should be considered in a possibly broadest sense and not to much importance should be attached to microscopic structural differences, while the species could be taken in a narrower sense for ecological and genetic purposes. This approach apart from the negative effects of such a divorce of taxonomy from ecology and genetics, involves the danger of distinguishing heterogenous complexes consisting of sibling species and pseudo-sibling species. We think like MAYR (1942, 1953) that sibling species should be recognized both by ecologists and geneticists and by taxonomists and they should be distinguished from races.

The difficulties caused by limiting the study to the general external morphology of the adults are due both to the lack of constant interspecific differences and to the wide scale of intraspecific and, above all, intrapopulational variability. It is the more so as the latter sometimes passes gradually from continuous to discontinuous variability — to polymorphism. Apart from sexual dimorphism which is typical of the genera *Ophiomyia* BRASCHN. and *Tylomyza* HEND. and of the subgenera *Nemorimyza* FREY and *Dizygomyza* HEND. s. str., cases of polymorphism independent of sex can be found among the *Agromyzidae*. This seems to be more often polymorphism in the strict sense than cyclomorphism, also called seasonal polymorphism or polymorphism of generations (cf. HENNIG, 1950). Different morphae prevail in different generations, probably as a result of the selective influence of environmental factors. Polymorphism in the *Agromyzidae* is polychromatism, because it is manifested in the coloration of certain external parts, such as the mesonotum, scutellum, pleurae, abdomen, legs or maxillar palpi. These features have been often considered to be of high taxonomic value. Distinct asexual polychromatism has been discovered so far in at least four species: *Cerodontha denticornis* (PANZ.), *Phytoliriomyza perpusilla* (MEIG.), *Phytomyza abdominalis* ZETT. and *Ph. ranunculi* (SCHRK.). *Cerodontha denticornis* (PANZ.) is differentiated into three morphae: the dark f. *nigroscutellata* STROBL, the light f. *semivittata* STROBL and an intermediate typical form, the first form being supposed to correspond to the hibernating generation (HENDEL, 1932). The two morphae of *Phytomyza abdominalis* ZETT. mining leaves of *Hepatica nobilis* GRSL. differ in the colour of the abdomen which according to HENDEL (1934) is yellow in its basal part in the hibernating generation and completely dark brown in the non-hibernating one (f. *socia* BRI.). From larvae mining in autumn (collected 12—14 X 1955 at Sieraków in the Kampinos-Forest) the author reared, however, both adult forms (1 ♂ and 2 ♀♀ on 6—9 XI 1955) and the form with the dark abdomen in spring of the next year (1 ♀ in IV 1956). *Phytomyza ranunculi* (SCHRK.) mining leaves of *Ranunculus* L. is found in four morphae: f. *praecox* MEIG., f. *flavoscutellata* FALL., f. *albipes* MEIG. and f. *flava* FALL. The first morpha (the darkest one) is supposed to be the hibernating generation, the next three morphae (successively lighter) belong to the non-hibernating generations. These colour forms were recognized as conspecific because they had been reared

from similar larvae feeding in similar mines and because intermediate individuals have been often found. This conspecificity has been reaffirmed by the author on a quite abundant material after examining the male copulatory apparatus [cf. Fig. 22].

To the above four known cases of asexual polymorphism we add here two further cases, namely in *Phytagromyza populi* (Kalt.) and *Phytomyza hieracii* Hend. According to Kaltenbach (1864) two colour forms of *Phytagromyza populi* (Kalt.) mining laeves of *Populus nigra* L. are annual generations. However, when the light form was reared by Hering (1925) in two generations, Hendel (1927) described the dark form as a distinct species — *Ph. populivora* Hend. But this was questioned by de Meijere (1928), when he had succeeded in rearing both the dark and the light form in the second generation from similar mines and larvae collected in the same place and at the same time. As the author had also reared the two colour forms together with intermediate individuals simultaneously from similar larvae and mines (collected at Kazuń near Warszawa, 7 X 1955; 1 ♂ emerged 27 X 1955, 5 ♂♂ and 9 ♀♀ — 4—6 V 1956) and as he found no differences in the copulatory apparatus of these forms, he thinks that they belong to the same species: *Ph. populi* (Kalt.). It must be noticed that the polychromatism of this species is parallel to the polychromatism of *Cerodontha denticornis* (Panz.) (f. *nigroscutellata* Strobl and f. *semivittata* Strobl) and to that of *Phytomyza ranunculi* (Schrk.) (f. *flavoscutellata* Fall. and f. *albipes* Meig.) as well as to the interspecific differences found within *Liriomyza* Mik, *Phytagromyza* Hend. and *Cerodontha* Rond.: there oblong dark stripes on the mesonotum either merge in one spot or are separated by light oblong lines [Fig. 3—6, cf. also Fig. 15 and 22]. Hendel (1935) took the colour differentiation of *Phytomyza hieracii* Hend. mining leaves of *Hieracium pilosella* L. for sexual dimorphism: he supposed that the males were light and the females dark. As the author has 1 ♂ and 1 ♀ (reared by Hering 9 and 14 III 1925 from larvae collected at Berlin-Frohnau) both in the light form (which is, after all, very similar to *Ph. analis* Zett.) he believes that polychromatism in *Ph. hieracii* Hend. is also independent of sex. It can be expected that more cases of polymorphism will be found in the *Agromyzidae* when male and female genitalia and larvae of all species, and particularly of the forms described on the basis of captured specimens, have been studied in detail.

While in certain cases the colour forms were taken for species, in other distinct species were regarded as morphae. It would seem from Hendel's and Karl's collections that some species of the group of *Liriomyza miki* (Strobl) were mistaken for coloured forms of *Phytoliriomyza perpusilla* (Meig.). Hendel (1931) had based the monotypic subgenus *Phytoliriomyza* Hend. on a single character only — the direction of the curvature of the orbital hairs. He did not notice, however, that the hairs were proclinated not only in *Phytoliriomyza perpusilla* (Meig.) but also in some other species which he

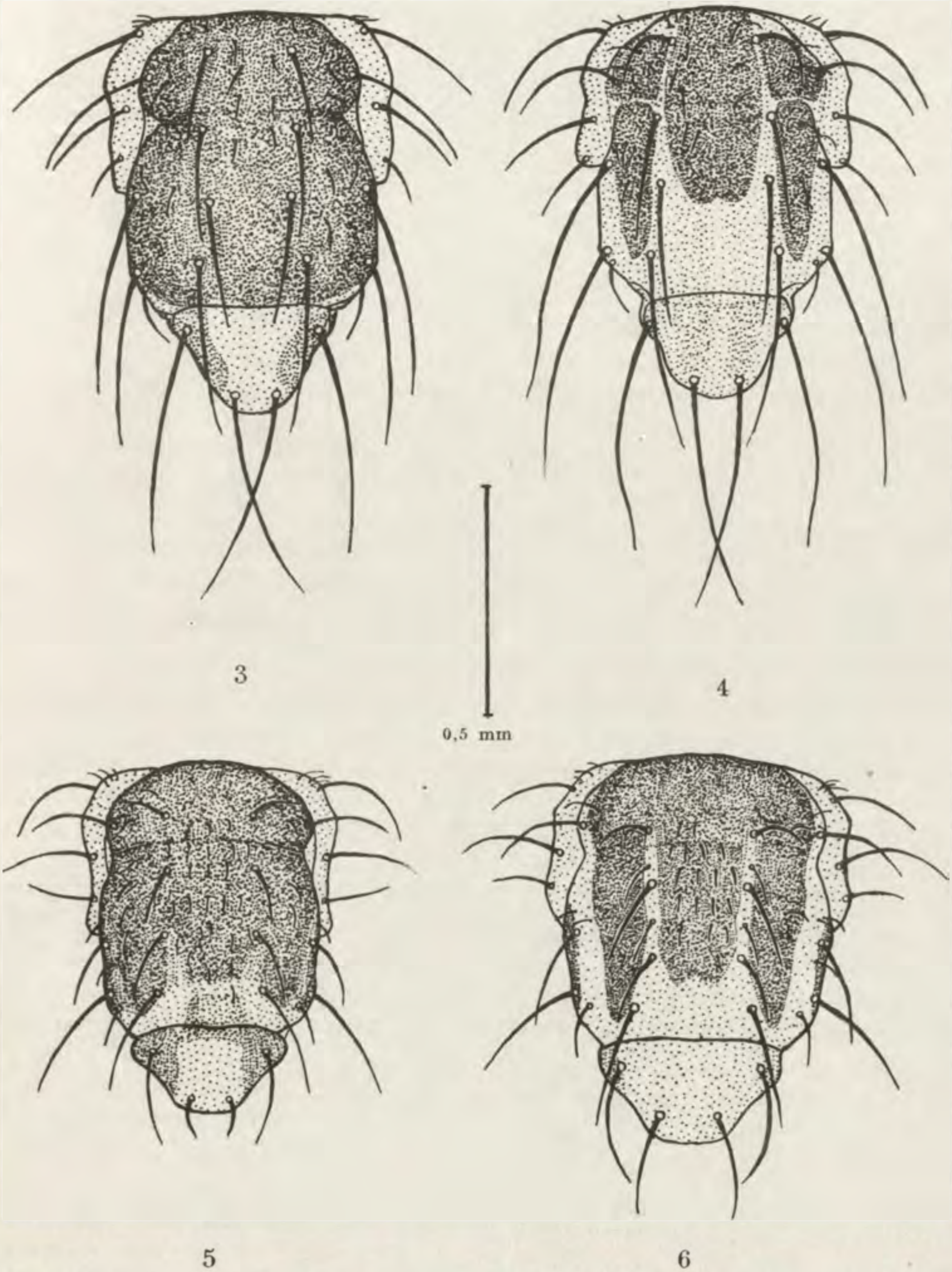


Fig. 3—6. Polychromatism. Thorax of: 3 — *Phytomyza ranunculi* f. *flavoscutellata* FALL (Kraków, 3 V 1891, leg. K. BOBEK), 4 — *Phytomyza ranunculi* f. *albipes* MEIG. (from *Ranunculus repens* L., Młociny at Warszawa, 14 VI 1955, leg. J. T. NOWAKOWSKI), 5 — *Phytagromyza populi* f. *populivora* HEND. (from *Populus nigra* L., Kazuń near Warszawa, 6 V 1956, leg. J. T. NOWAKOWSKI), 6 — *Phytagromyza populi* (KALT.) (from *Populus nigra* L., Kazuń, 6 V 1956, leg. J. T. NOWAKOWSKI).

classified as *Liriomyza* MIK. This was probably caused by the small number and the weak development of the orbital hairs in the species mentioned. They have in fact little in common with *Phytoliriomyza perpusilla* (MEIG.) but specimens of these species are often placed erroneously together with it as one polymorphic species. The light morpha of *Ph. perpusilla* (MEIG.) is placed together with *Liriomyza striata* HEND., a whole series of which we found in KARL's collection (from the district Słupsk in the Polish Pomerania, 1 ♂ captured on 16 VII 1921, 1 ♂ — on 4 VIII 1921, and 1 ♀ — on 25 VI 1921) among specimens of the former species represented by the dark morpha.

Summing up it should again be stressed that the general external morphology of the adults is not sufficient to distinguish species or to determine their natural relationship and in the case of so-called difficult groups it is generally of rather little taxonomic value. To limit the approach to this only aspect would mean to employ an inadequate method of investigation and it would give a very obscure picture of reality. It would make one completely doubt the reality of species and the possibility to discover their natural relationship and thus put under doubt the whole sense of systematic investigations. Identification of an adult according to its external morphology must be regarded in many a case as a mere introduction which must be followed by a more reliable identification based on its genital apparatus.

The Male Genital Apparatus

The great importance of the male genital apparatus for the classification of the *Agromyzidae* was foreseen already by HENDEL (1931) and SÉGUY (1934). Nevertheless, these structures have not so far been used for taxonomic purposes, probably because of their extreme complexity and the absence of a general morphological interpretation of their particular parts. A first attempt to illustrate and describe these organs was made by SÉGUY (1934), but it was FRICK (1952) who described them in detail in a species from the group of *Agromyza rufipes* MEIG. (identified as *A. reptans* FALL). Descriptions of the terminalia of the particular genera by FRICK and his key to the genera based on the terminalia were not, however, completely successful. Figures (sometimes together with descriptions) ot the male genitalia were also given after 1930 — but not with equally successful results — by the following authors: CIAMPOLINI (1952) — in *Pseudonapomyza dianthicola* VENT., FROST and SASAKAWA (1954) — in *Phytomyza jucunda* FROST et SASAK., GRIFFITHS (1957) — in *Phytomyza adjuncta* HER. and *Ph. melana* HEND. and later (1959) — in *Ph. affinis* FALL., HENDEL (1931) — in *Phytomyza ranunculi* (SCHRK.), *Ph. plantaginis* R. D., *Ph. tenella* MEIG., *Ph. albiceps* MEIG. and later (1932) —

in "*Phytagromyza spinicauda* HEND." [= *Ph. flavocingulata* (STROBL), cf. p. 100], HENNIG (1958) — in *Encoelocera bicolor* LOEW, HERING (1951c) — in *Agromyza cinerascens* MACQ. and *A. vèris* HER. and later (1957a) — in A. *reptans* FALL. and *A. buhriella* HER. and recently (1958b) — in *Phytomyza araciocecis* HER. and *Ph. crepidocecis* HER., KANGAS (1949) — in *Dendromyza barnesi* HEND. and *D. betulae* KANG., MELIS (1935) — in *Phytomyza atricornis* MEIG., NIETZKE (1943) — in *Cephalomyza cepae* (HER.), NOWAKOWSKI (1958) — in *Phytomyza campanariae* NOWAK. nad *Ph. ranunculivora* HER. and later (1960a) in *Irenomyia obscura* (ROHD.-HOLM.) and *Xeniomyza ilicitensis* HER. in MEIJ. and recently (1960b) in *Agromyza celtidis* NOWAK. and (1961) in *Liriomyza heringi* NOWAK., SASAKAWA (1953, 1954, 1955) — in *Agromyza spiraeae* KALT., *Phytomyza senecionis ravasternopleuralis* SASAK. and 15 other species known only from Japan, SÉGUY (1934) — in *Agromyza rufipes* MEIG. and *Phytomyza ranunculi* (SCHRK.) (identified as "a species of the group of *Ph. vitalbae* KALT."), SÉLLIER (1947) — in *Liriomyza mesnili* D'AGUILAR, VENTURI (1935) — in *Pooemyza lateralis* (MACQ.) and later (1936) in *Agromyza mobilis* MEIG. In his revision of the group of *Phytomyza obscura* HEND. NOWAKOWSKI (1959) attempted also a general description of the male copulatory apparatus [Fig. 7]. This attempt concerns the majority of the species groups now included in the genus *Phytomyza* FALL. s. str., and it contains figures and descriptions of the male genitalia in 9 species: *Phytomyza obscura* HEND., *Ph. origani* HER., *Ph. tetrasticha* HEND., *Ph. nepetae* HEND., *Ph. lycopi* NOWAK., *Ph. lithospermi* NOWAK., *Ph. pulmonariae* NOWAK., *Ph. symphyti* HEND. and *Ph. myosotica* NOWAK.

In studying the male genital apparatus of the *Agromyzidae* the impression of monotony given by the external morphology of the adults disappears completely. A most surprising fact is the enormous differentiation of shapes which more than compensates for the poor external differentiation. It can be seen that the chief morphological effect of the divergent evolution of the adults is shown in changes of the genital apparatus, while changes in the external skeleton reflect it relatively weakly.

The problem of the taxonomic value, i. e. of the specificity of the genitalia in insects is connected with the significance of the so-called mechanical isolation for the speciation and for the conservation of species. DUFOUR (1844) was the first to say that: "l'armature copulatrice est la garantie de la conservation des types, la sauvegarde de la legitimité de l'espèce" and that it "varie comme les espèces". JORDAN (1905, cf. ALLEE, 1949) developed this dea further and put forward the "lock-and-key" theory, according to which the adjustment of the copulatory organs of both sexes is peculiar to the particutlar species and consequently each essential change in the genitalia should result in reproductive isolation. Thus, the very definition of the species as interbreeding community shows the importance of the copulatory apparatus.

More recent authors (DOBZHANSKY, 1941; HENNIG, 1950; VAN EMDEN, 1953) admit the great role of the genitalia in the taxonomy of insects but they try

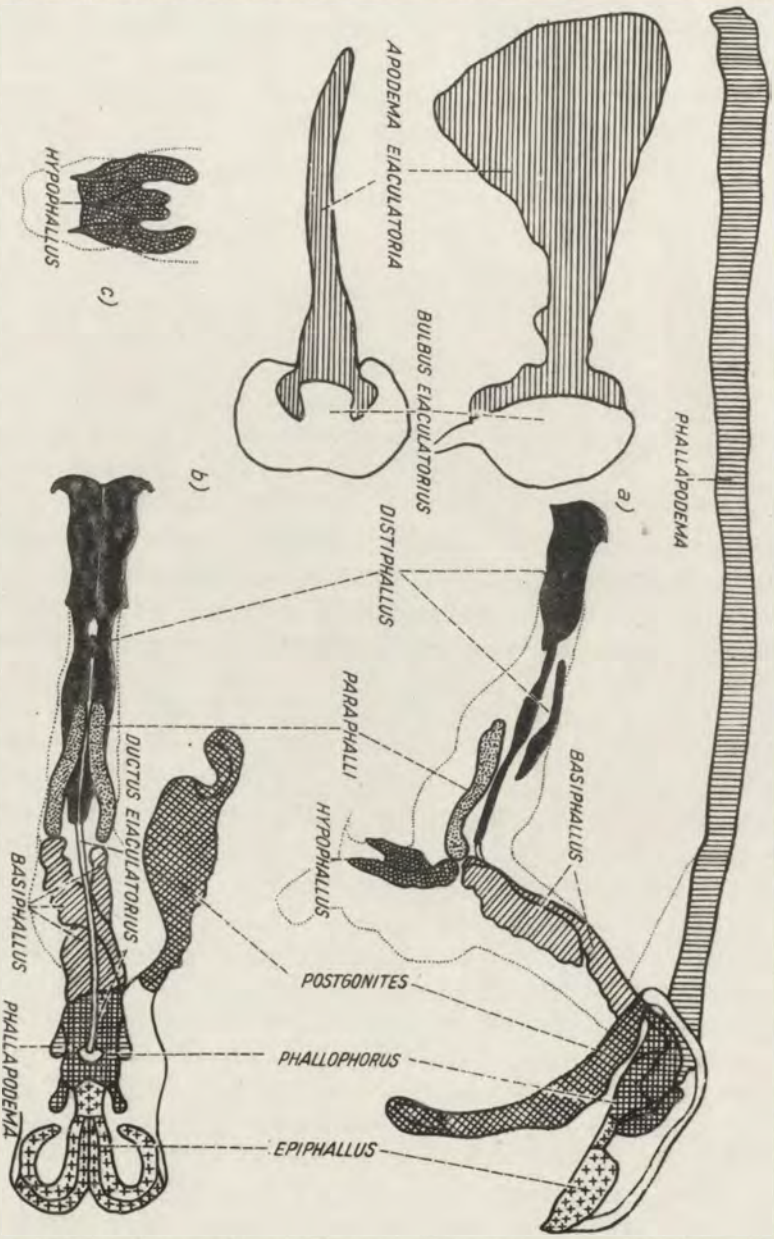


Fig. 7. Schematic sketch of the male copulatory apparatus of *Phytomyza tetrasticha* HEND. (after removal of the epandrium and hypandrium together with their appendices): a — from the side, b — from below, after removal of the right postgonite, hypophallus and phallapodeme, c — hypophallus from behind (after NOWAKOWSKI, 1959, modified).

to explain it differently rejecting the "lock-and-key" theory and minimizing the importance of mechanical isolation. DOBZHANSKY (1941) points out the correlation between the taxonomic value of the genitalia and the degree of their complexity. He goes to believe that it is only because of greater complexity of genitalic characters as compared with external ones that genetic interspecific differences manifest themselves in a more striking way in the genitalic characters than in the external ones. The genitalic differences are not the original cause of biological isolation but they result from speciation directed by other isolating mechanisms. VAN EMDEN (1953) quotes numerous observed facts of copulation of representatives of different species and genera. The genitalic differences are too small to prevent such copulation and insemination, and in addition, hybrids of species with quite different sexual armatures were also obtained. A generally much lower degree of differentiation of the genitalia of females than those of males, together with cases of a wide intraspecific variability of the genitalia, and finally, the lack of clear differentiation of them in some groups of insects, contradict the concept of the mechanical isolation. According to VAN EMDEN the very great importance of the male genitalia of *Diptera* for the systematist lies "not so much in any basically greater contribution made by them to the creation of the phenotype of a fly but rather in the fact that they constitute a large complex of additional characters, which allows to supplement and check results obtained from other characters, much as the structure of the early stages and the anatomy afford new means for checking the classiffication".

While in principle we share these wiews, we feel, however, the lack of some more convincing explanation of the relative intrapopulational stability of genitalic structures as compared with other morphological characters. This is very often observed in entomological practice and it occurs in a striking way in the group of insects discussed here. First of all, the genitalia are not subject to discontinuous variability as are some external characteristics of the adult and larva, i. e. to polymorphism (in the strict sense) and cyclomorphism[1]. Moreover, a large range of continuous variability could be expected in plastic and complex organs. In this respect, the genital apparatus will apear to be, in fact, of an as variable nature as chaetotaxy or coloration, if we attribute the same value to all details of its structure. The evaluation of the genitalic characters shows, however, that apart from some rather variable parts, such as apodemes or membranes, there are relatively few variable, very specific parts. They are the slerites of the aedoeagus, especially the apical ones.

This specificity of the parts of the male genital apparatus, which in copulation enter the genitalia of the female seems to give evidence of the role of the mechanical isolation in the species-formation and conservation. Mechanical

[1] Rare cases of cyklomorphism of the genitalia are known only among the *Coleoptera* and *Homoptera*.

isolation must not, however, be interpreted as a sort of constant intangible barrier but rather as a negative factor of sexual selection, the effect of which can be seen in a population scale. The differences in the structure of the aedoeagus, especially in closely related species, are decidelly too small to prevent copulation but even slight mechanical obstacles in the act, connected with certain sensuous inhibitions will reduce the probability of interbreeding of individuals with not quite adjusted genitalia. Denying of the significance of these minor deviations would amount to denying the role of natural and sexual selection.

Ideas admitted by the author on the basis of the group examined are in agreement with PETERSEN's concepts (1927, 1930) of the significance of sexual organs in mining moths. PETERSEN believes the morphological differentiation of the sclerotized parts of the aedoeagus to occur above all at the splitting of species. That is why "die Sexualarmatur besonders beim ♂ so charakteristisch für jede Art ist, dass nur in ganz seltenen Fällen die Feststellung der Art auf Schwierigkeiten stösst". On the other hand, external morphological features are often graded in a very subtle way and not necessarily go alongside with biotic features. "Die Art ist eine Geschlechtsgenossenschaft, die Zugehörigkeit zu derselben findet neben anderen morphologischen Eigenschaften ihren präzisesten Ausdruck in den Generationsorganen".

The high degree of correlation of genitalic features with essential biotic characters of mining flies species is an indication of the high taxonomic value of the genitalia. The term "genitalic species" may be used here for working purposes because a definite copulatory apparatus corresponds, as a rule, to a definite larval form and a definite feeding pattern on a definite host plant. The external structure of the adult insect, on the other hand, does not show such a clear correlation with larval morphology and ecology. That is why we think that the structure of the genitalia is neither merely "one more additional criterion", nor even "an absolute criterion decisive in all cases", but that it is one of the principal and essential taxonomic criteria.

The contradiction between the "evolutioanry plasticity" of the genitalia and their "small intraspecific variability" is only an alleged one. The variability of the genitalia is more interpopulational than intrapopulational. It is here actually or potentially species-forming and signalizes the splitting of the species. On the other hand, variability of the external characters does not exactly reflect the process of speciation and it may even be unconnected with it (polymorphism, cyclomorphism, some ecotypes and ecophenotypes, some directional variations, cf. pp. 132—133).

A study of the copulatory apparatus makes it possible in most cases to distinguish quite easily species which examined only in their external characters seem to be identical or indistinctly separated. This is evident particularly in such "difficult" groups, as the subgenera *Dizygomyza* HEND. s. str., and *Pooemyza* HEND., the complex of *Liriomyza pusilla* (MEIG.), of *Phytomyza*

obscurella FALL. (cf. GRIFFITHS, 1957), *Ph. obscura* HEND. (cf. NOWAKOWSKI 1959), *Ph. albiceps* MEIG., *Ph. affinis* FALL. etc. Sometimes what we have considered to be one species appears to be a complex of "genitalic species". Thus, e. g. *Phytomyza obscura* HEND. s. l. has proved to be a complex of five species, *Pooemyza muscina* (MEIG.) — a complex of two species, *Agromyza rufipes* MEIG. — a complex of at least two species, *Phytomyza abdominalis* ZETT. — a complex of three species. In most cases they are sibling species, sometimes, however, they show such different types of copulatory apparatus that they must be called "pseudo-sibling species". E. g. *Phytomyza obscura* HEND. s. l. (on *Labiatae*) comprises two different species groups. The first of them includes: *Ph. obscura* HEND. s. str. (on *Satureja* L. s. l.), *Ph. origani* HER. (on *Origanum* L.) and *Ph. tetrasticha* HEND. (on *Mentha* L.) — the second: *Ph. nepetae* HEND. (on *Nepeta* L.) and *Ph. lycopi* NOWAK. (on *Lycopus* L.) (cf. NOWAKOWSKI, 1959).

On the other hand, an examination of the copulatory apparatus sometimes shows conspecificity of forms formerly regarded as distinct species, especially in cases when, contrary to the original description, it was impossible to find clear differences in the external morphology of adults. After examining some type-specimens from HENDEL's collection the author has come to the conclusion that at least seven specific names introduced by this dipterologist and one given by MEIGEN and accepted by HENDEL are junior synonyms of other names, thus:

Amauromyza strobli HENDEL, 1920	= *A. abnormalis* (MALLOCH, 1913)
Amauromyza balcanica HENDEL, 1931	= *A. morionella* (ZETTERSTEDT, 1848)
Cerodontha femoralis (MEIGEN, 1838)	= *C. fulvipes* (MEIGEN, 1830)
Liriomyza orbonella HENDEL, 1931	= *L. orbona* (MEIGEN, 1830)
Liriomyza subobliqua HENDEL, 1931	= *L. obliqua* HENDEL, 1931
Pooemyza semiatra HENDEL, 1931 = *Phytagromyza spinicauda* HENDEL, 1920	= *Ph. flavocingulata* (STROBL, 1909)
Phytagromyza tristriata HENDEL, 1932	= *Ph. trivittata* (LOEW, 1873)

If there are distinct external differences, the lack of any differentiation of the terminalia is not sufficient to justify synonymization, the identity of the larvae and their mines should also be verified in such cases.

Finally, a study of the copulatory apparatus makes it possibile to identify captured male specimens, revealing at the same time misidentifications of a considerable number of specimens found in collections. Thus, an immediate task for specialists is to describe carefully and methodically and give figures of the male genitalia of all known species of the *Agromyzidae* and to prepare a key based on genitalic characters too.

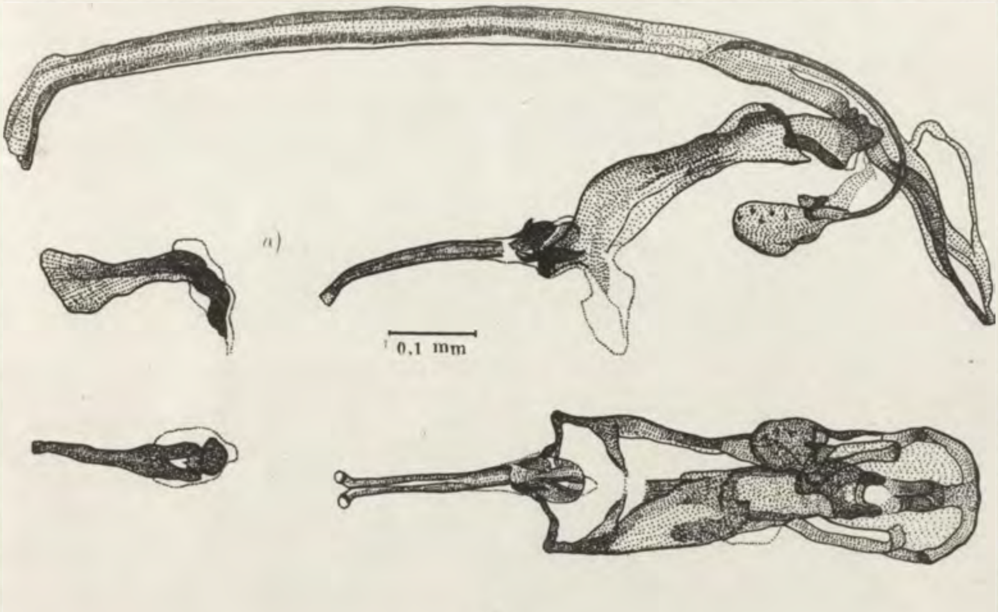
Original descriptions and figures should be based on reared male specimens previously identified not only according to their external morphology but also according to their larvae and the mines. If the genitalia of captured specimens are described (without any comparison with the genitalia of reared

ones) repeated misidentifications and confusions may result. It may be recalled in this connection that a specimen which served FRICK (1952) to his general description and illustration of the male terminalia in the *Agromyzidae* was identified by him as *Agromyza reptans* FALL., although it must have belonged to one of the "genitalic species" of the group of *Agromyza rufipes* MEIG. living on *Boraginaceae* and regarded as one oligophagous species. Some species of this group are very difficult to distinguish externally from *Agromyza reptans* FALL. which feeds on *Urticales* and the copulatory apparatus or which is of quite a different type [Fig. 8–9].

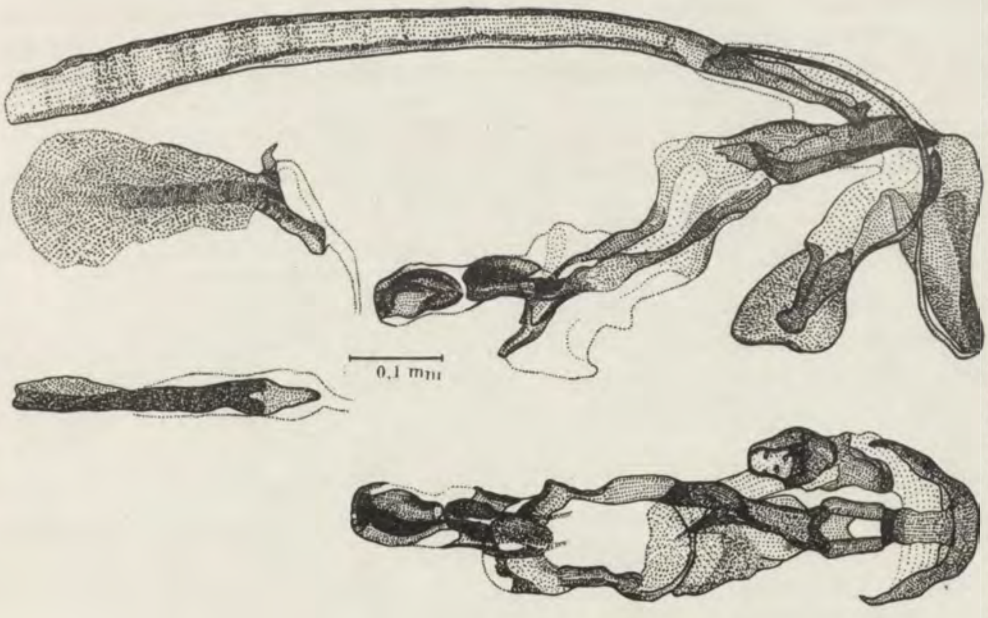
Male genitalia in species, the types of which are captured specimens, must be examined and described on the basis of these types. This will give, at the same time, a verification of the names of these species. It can be expected that a number of names will prove to be junior or senior synonyms of names based on reared types. It is also not unlikely that certain reared specimens were erroneously included under certain names based on captured type-specimens. This is why every "elucidation of the ecology of a species" should be verified. We hope that in future good specialists will avoid descriptions based on captured material and without taking account of the terminalia.

A knowledge of the copulatory apparatus is not only very important for distinguishing species but is also absolutely necessary for establishing their relationship and building the natural system of the group. Our conviction of the fundamental role of the genitalia of the *Agromyzidae* in the investigation on their phyletic relationship is supported mainly by the extremely complex structure of these organs. The "criterion of complexity" is one of the criteria of phyletic relationship (HENNIG, 1950) or of the homology which is, in fact, coresponding to it: "Die Sicherheit" (der Homologie) "wächst mit dem Grad der Komplikation und Übereinstimmung der vergliechenen Strukturen" (REMANE, 1952). Another argument is the large size of the terminalia, as compared with the size of the whole body; they may occupy almost half of the abdomen, and their sclerotized parts prevail over the soft ones.

The external skeleton of the mining fly, with all its structures, is in fact more complex than the copulatory apparatus but is far less differentiated within the group. This monotony arises not only from the conservatism of many characters of the external skeleton but it is caused as well by parallel evolution of its more plastic features — chaetotaxy and wing venation (cf. pp. 116–123) and probably by parallelism or reversibility in the evolution of some colour features. Thus, an alternative to the intricate complex of genitalic characters are generally single simple external characters. In other words, the probability of multiple independent occurrence of an essentially similar structure of a very complex genital apparatus is much smaller than the parallelism in certain external details which were considered to be taxonomically valuable (cf. also p. 132–133). Individual details of the genitalia show, of course, some parallelisms as well.



8



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Fig. 8–9. "Pseudo-sibling species". Male copulatory apparatus of: 8 – *Agromyza reptans* Fall. (Galicia, XIX cent., leg. M. Nowicki). 9 – *Agromyza rufipes* Meig. s. l. (Galicia, 1867, leg. M. Nowicki).

In checking external characters by the genitalic ones we replace a clearly artificial system by a more natural one, more coordinating adult with larval features and morphological with ecological features, and thus, giving some picture of the evolution of the group. Species of an essentially similar type of the genital apparatus form groups corresponding to natural genera. Representatives of the same natural genus or subgenus are usually found on related host plants, much more rarely on the same plant, and in most cases they mine in a similar way. Adults show rather poor external differentiation. If larval spiracles are considerably differentiated, this differentiation is parallel in various natural genera. Parallel series of increasing apomorphy in larval characters are observed (cf. pp. 124—128).

As it has already been mentioned, there is no doubt that all the existing limits of large genera of the *Agromyzidae*, and at least of the *Phytomyzinae* are artificial. These genera comprise sometimes over hundred species and differ only in single external features such as the coloration of the halteres or of the scutellum (which is, after all, variable within some species), the direction of curvature of the orbital hairs or characters of wing venation which became reduced quite independently in many phyletic lines. No wonder that limits of such genera are supported neither by the larval morphology (cf. DE MEIJERE, 1950), nor by the morphology of the male terminalia. Each of these artificial genera comprises a larger or smaller number of sometimes quite unrelated natural genera. Some of these natural genera are split by the limits of the artificial genera. The grouping of species within these large genera varies with every author and is not always in agreement with the natural classification.

In spite of HENDEL's view (1931) even *Liriomyza* MIK does not seem to be a strictly monophyletic group and it is not well separated from all the other genera, especially from *Phytobia* LIOY s. l. (sensu FRICK) (= *Dizygomyza* HEND. s. l.) being a conglomerate of various natural groups. As the basis of delimitation of *Liriomyza* MIK from *Phytobia* LIOY s. l. serves the yellow coloration of the scutellum in the former genus. This however, was already weakened by NIETZKE (1943) who described the so-called "Herxheim race" of *Phytobia* (*Cephalomyza*) *cepae* (HER.), which differs from the "Oggersheim race" (nominal subspecies) by its yellow coloration of the middle part of the scutellum. Thus, it was proved in this case that the limit between two genera runs intraspecifically (or right through a group of sibling species). Examination of the male genitalia finally convices us that this limit is artificial and that *Cephalomyza* HEND. should be included in the genus *Liriomyza* MIK rather than in *Phytobia* LIOY s. l.

Also the subgenus *Praspedomyza* HEND. belongs rather to *Liriomyza* MIK, with the exception of *P. hilarella* (ZETT.) mining leaves of *Pteridium aquilinum* L. (KUHN) (*Polypodiaceae*), which was already defined by HENDEL (1931) as an isolated species. This unique miner of ferns within *Phytobia* LIOY

s. l. has quite a specific sexual armature and that is why we designate it as the type of a new genus *Pteridomyza* gen. nov.

The remaining subgenera of *Phytobia* Lioy s. l. living on *Dicotyledones*, namely *Phytobia* Lioy s. str., *Nemorimyza* Frey, *Amauromyza* Hend., *Trilobomyza* Hend. and *Calycomyza* Hend., should be raised to the rank of genera. The natural genus *Calycomyza* Hend. seems to be connected rather with the *Compositae* only. Frick (1956) has included here a number of non-Palaearctic species feeding on many other plant families but his revision does not cover the terminalia. At least the dark coloured *C. gyrans* (Fall.) feeding on the *Campanulaceae* has quite a different and specific sexual armature and thus we designate it as the type of a new genus called *Campanulomyza* gen. nov.[1] Species of *Calycomyza* Hend. mining leaves of *Compositae* present a type of genitalia similar to that which is widespread in the complex of *Liriomyza pusilla* (Meig.) comprising above all numerous miners of *Compositae* too.

Because of clear biotic specificity: larvae feeding in the cambium of tree trunks, Kangas (1937, 1939) proposed to raise the rank of the subgenus *Phytobia* Lioy s. str. (= *Dendromyza* Hend.). *Dendromyza posticata* (Meig.) mining leaves of *Solidago* L. and *Aster* L. (*Compositae*), which had been included in this group by Hendel (1931), was already separated by Frey (1946) as a monotypic subgenus called *Nemorimyza* Frey. Comparison of the copulatory apparatus fully confirms this and even justifies the raising of the taxonomic rank of both these subgenera.

One of the reasons why the existing classification of the *Agromyzidae* is artificial is that large groups have been distinguished on the basis of characters which evolved in a directional and parallel way. Such are first of all certain characters of the wing venation. The terminal section of the costa, contained between r_{4+5} and m_{1+2}, as well as the posterior transverse vein (t_p) are independently reduced in many phyletic lines and thus the division into genera on the basis of these characters is a horizontal rather than a vertical one (cf. pp. 117—121).

It was Enderlein (1936) who excelled in making such horizontal divisions and who established or at least restored certain artificial genera, without even designating their types. Thus, the genus *Domomyza* Rond. rejected by de Meijere (1925) and Hendel (1927) comprised representatives of *Agromyza* Fall., with the costa reaching only to r_{4+5}. Examination of the male genitalia shows that these species belong to three different natural groups: that of *Agromyza nana* Meig. (on *Leguminosae*), of *A. cinerascens* Macq. and of *A. ambigua* Fall. (on *Gramineae*). To the group of *A. ambigua* Fall. which is unrelated to the two first groups belong not only species enumerated by

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[1] This species was recently included by Hering (1960) into his new genus *Melanophytobia* Her. Through the kindness of Prof. Hering we were able to investigate the male genital apparatus of its type-species, *M. chamaebalani* Her., and we stated this species not to be congeneric with *Campanulomyza gyrans* (Fall.) but rather with *Irenomyia obscura* (Rohd.-Holm.) living also on the *Leguminosae*.

Hendel (1931) on pp. 95–96, sec. 16–23, and *A. bicaudata* Hend. placed by him in sec. 46, but also *A. veris* Her. which was included by Hering (1951 c) rather in the group of *A. cinerascens* Macq. In fact, Enderlein (1936) limited *Domomyza* Rond. to the group of *A. nana* Meig. but from the rest of this taxon he established an artificially delimited genus *Stomacrypolus* Enderl. comprising the group of *A. cinerascens* Macq. and a part of the group of *A. ambigua* Fall.

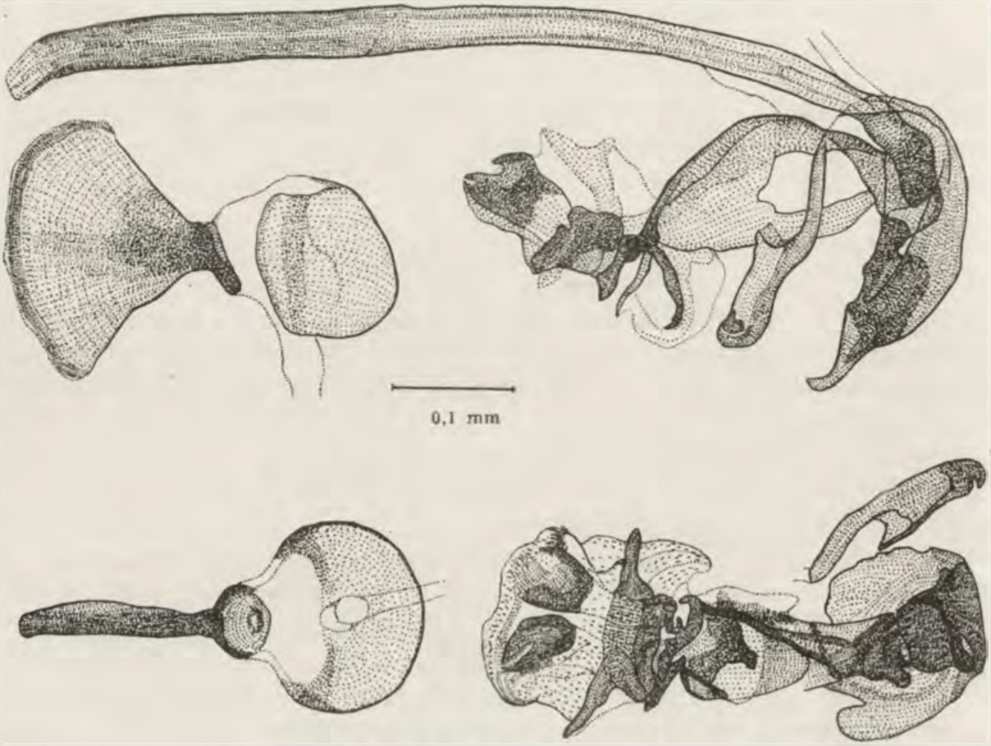
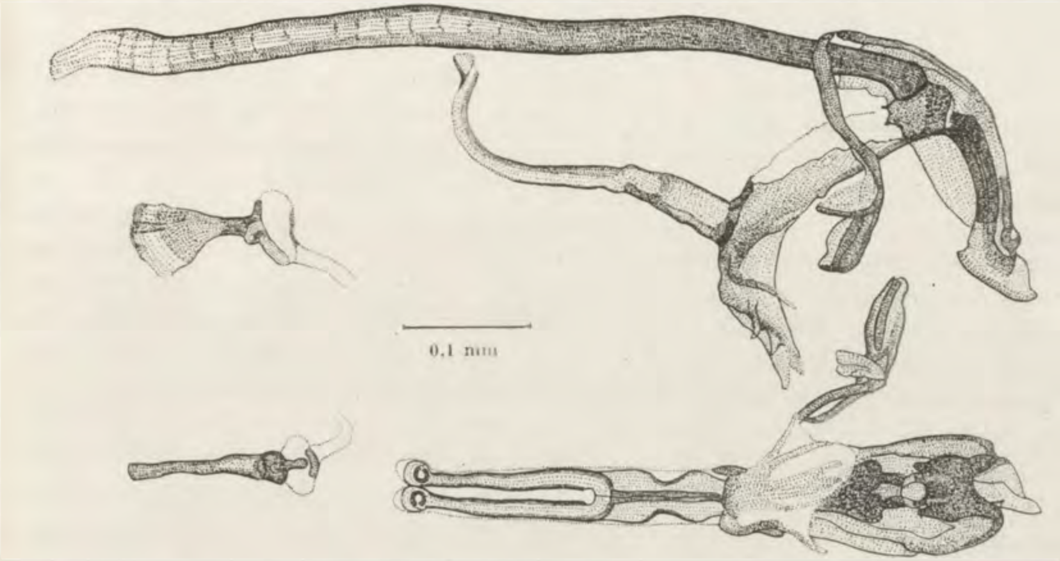


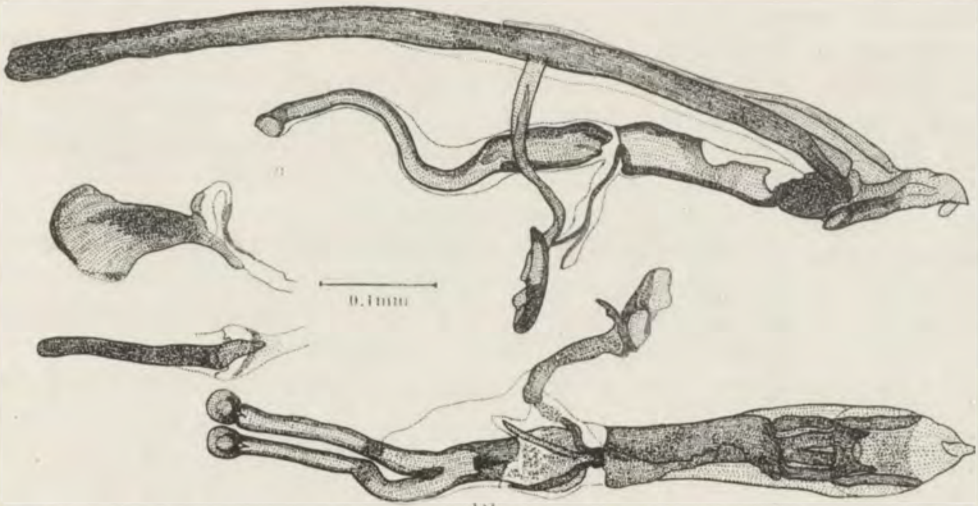
Fig. 10. Male copulatory apparatus of *Amauromyza lamii* (Kalt.) (from *Betonica officinalis* L., Kampinos Forest, Cybulice 19 VIII 1956, leg. J. T. Nowakowski).

Criticizing Enderlein's system (1936) Hendel (1936) proved that in view of the parallel and orthogenetic reduction of the wing venation neither the extent of the costa nor the presence or absence of the t_p could be diagnostic of genera. He did not, however, fully realize his idea and left the artificial divisions between *Phytobia* Lioy s. l. (= *Dizygomyza* Hend. s. l.) and *Phytagromyza* Hend. and between *Napomyza* Hal. in Westw. and *Phytomyza* Fall. s. str. Frick (1952) shared Hendel's view, however, not only did he preserve these two artificial divisions but he also raised the subgenus *Napomyza* Hal. in Westw. to generic rank.

The basis of the division into *Phytobia* LIOY. s. l. and *Phytagromyza* HEND. is the extent of the costa combined with the lenght ratio of the sections of m_{3+4}, the latter being correlated with the distance between t_p and the base of the wing. SPENCER (1957a), however, was right when he did not apply this



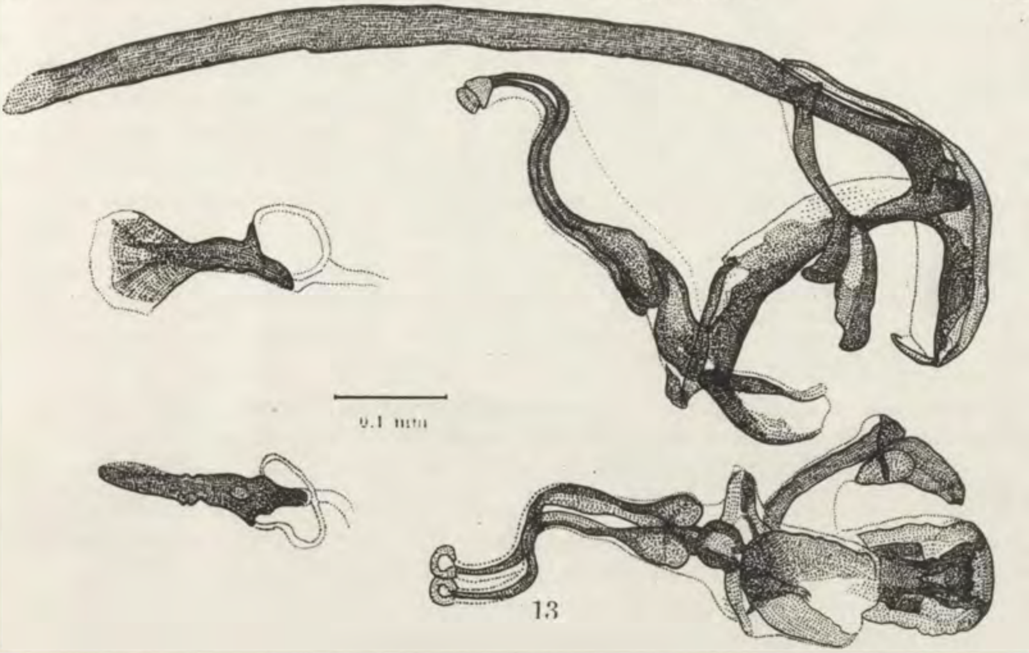
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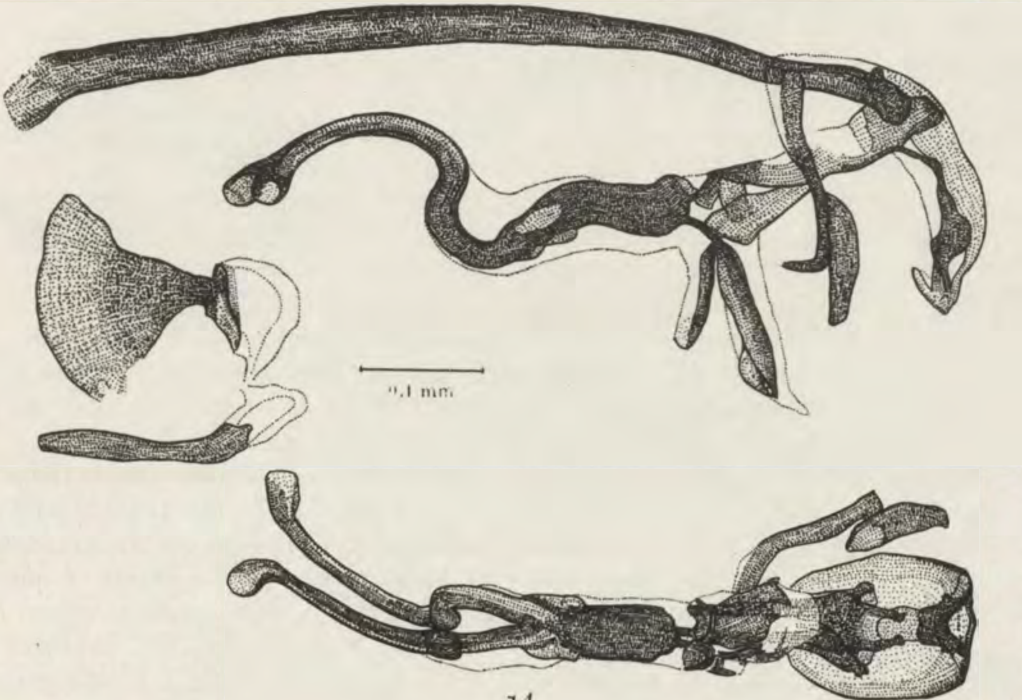
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Fig. 11–12. Artificial character of the existing division into *Phytobia* LIOY s. l. and *Cerodontha* ROND. Male copulatory apparatus of: 11 — *Icteromyza geniculata* (FALL.) (Kraków, 23 X 1885, leg. A. WAGA), 12 — *Cerodontha denticornis* (PANZ.) (Polish Pomerania, Słupsk, 22 VIII 1924, leg. O. KARL).

principle and included in *Amauromyza* Hend. the species *A. madrilena* Spenc., a miner of the *Labiatae*, which according to Hendel's and Frick's classification should be included rather in *Phytagromyza* Hend. The artificial nature of the existing division into *Phytobia* Lioy s. l. and *Phytagromyza* Hend. was also observed by the author, while examining miners of Monocotyledons. The subgenera *Icteromyza* Hend., *Dizygomyza* Hend. s. str., and *Pooemyza* Hend. feeding on Monocotyledons form one natural group with characteristically constructed genitalia [cf. Fig. 11, 13, 66, 67]. The group has, on the one hand, a close relationship with the whole genus *Cerodontha* Rond. [Fig. 12] and, on the other hand, a close relationship with *Phytagromyza flavocingulata* (Strobl) [= *Ph. graminearum* Her. = *Ph. spinicauda* Hend. = *Ph. ensifera* Her. = *Phytobia* (*Pooemyza*) *semiatra* (Hend.)] also feeding in leaves of grasses [Fig. 14]. De Meijere, who described the larva of this species as "*Dizygomyza* spec." (1934), already pointed out (1938) its affinity to *Pooemyza* Hend. We may assume now that the species belongs to *Pooemyza* Hend. not only because of certain larval characters (the group of processes over the mouth hooks), ecological (feeding on *Gramineae*) and external adult characters (a high and narrowed lunule) but also because of its copulatory apparatus which markedly resembles the apparatus of most representatives of *Pooemyza* Hend. mining grasses [cf. Fig. 13—14]. We may add, by the way, that two males of *Phytagromyza flavocingulata* (Strobl) in O. Karl's collection [captured near Słupsk (Stolp) in Polish Pomerania on 9 VI and 5 VII 1924] are identified as "*Dizygomyza incisa* Meig." and that the type of *Phytobia* (*Pooemyza*) *semiatra* (Hend.) we examined (captured by Kertesz on 2 VI 1904 at Mehadia in Hungary) is a specimen of *Ph. flavocingulata* (Strobl) too. The differences between *Phytagromyza flavocingulata* (Strobl) and *Pooemyza* Hend. consist only in the shortening of the costa to the distal end of r_{4+5} [Fig. 30—31] and a multiplication of the number of spiracular bulbs of the larva up to 18. These are exactly characters that evolve in a directional and parallel way (cf. pp. 117—119, 123—128). In many specimens of *Ph. flavocingulata* (Strobl) t_p has not been even distinctly shifted in the proximal direction and the last section of m_{3+4} is twice as long as the preceding one only in connection with a more lenghtened wing [Fig. 31]. The specimens of *Ph. flavocingulata* (Strobl) with the most distal location of t_p were described by Hering (1951b) as *Phytagromyza ensifera* Her., while the specimens with the most proximal location of t_p were described by Hendel (1931) as *Ph. spinicauda* Hend. As far as the genus *Cerodontha* Rond. is concerned, most of its representatives also live on *Gramineae* and it is only *C. lateralis* (Zett.) which was captured on *Juncus effusus* L. (*Juncaceae*) together with specimens of *Icteromyza capitata* (Zett.) (Hering, 1956a; de Meijere, 1941). *Cerodontha* Rond. differs, in fact, from *Phytobia* Lioy s. l. only in the lack of basal scutellar bristles (*b. sc*) because the horn or claw on the third antennal joint are not found in *C. atronitens* (Hend.) anp *C. biseta* (Hend.). These species were taken by Frey



13



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Fig. 13—14. Artificial character of the existing division into *Phytobia* LIOY s. l. and *Phytagromyza* HEND. Male copulatory apparatus of: 13 — *Pooemyza incisa* (MEIG. s. l.) [from *Agropyron repens* (L.) P. B., Kampinos Forest, Granica, 11 V 1956, leg. J. T. NOWAKOWSKI], 14 — *Phytagromyza flavocingulata* (STROBL) (from *Dactylis glomerata* L., Młociny at Warszawa, 23 IV 1957, leg. J. T. NOWAKOWSKI).

(1946) as a distinct subgenus called *Xenophytomyza* Frey, because they seemed to him to resemble the dark coloured species of *Dizygomyza* Hend. s. l. *C. biseta* (Hend.) was even originally described as a representative of *Dizygomyza* Hend. s. l. Thus, finally by including to *Cerodontha* Rond. a considerable part of the artificial genus *Phytobia* Lioy s. l. (subgenera: *Icteromyza* Hend., *Dizygomyza* Hend. s. str. and *Pooemyza* Hend.) and also *Phytagromyza flavocingulata* (Strobl) the author forms a large natural genus living on *Monocotyledones* (*Gramineae*, *Cyperaceae*, *Juncaceae*, *Iridaceae*). Henceforth, the name "*Phytobia* Lioy" should be treated as a senior synonym for "*Dendromyza* Hend."

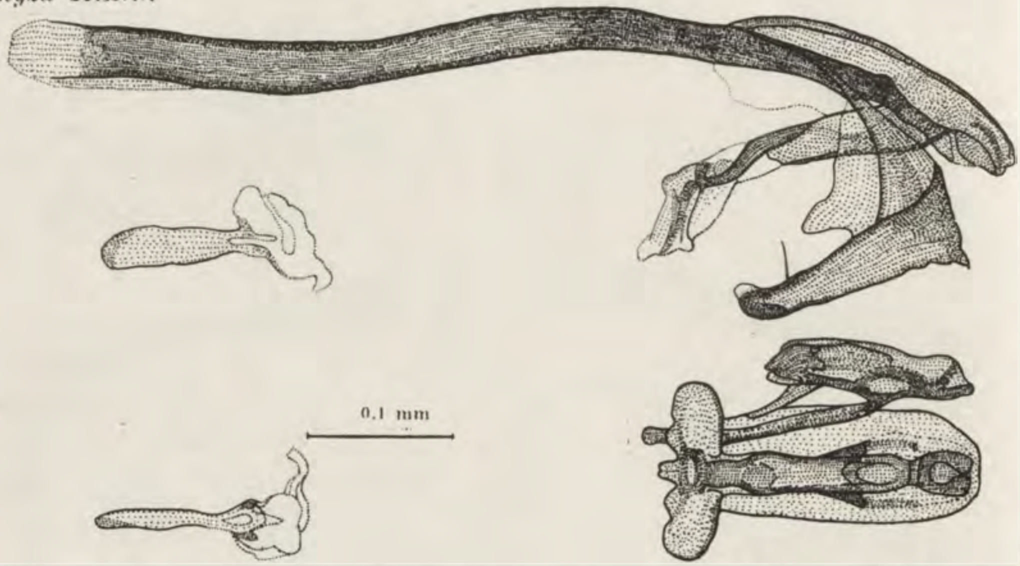
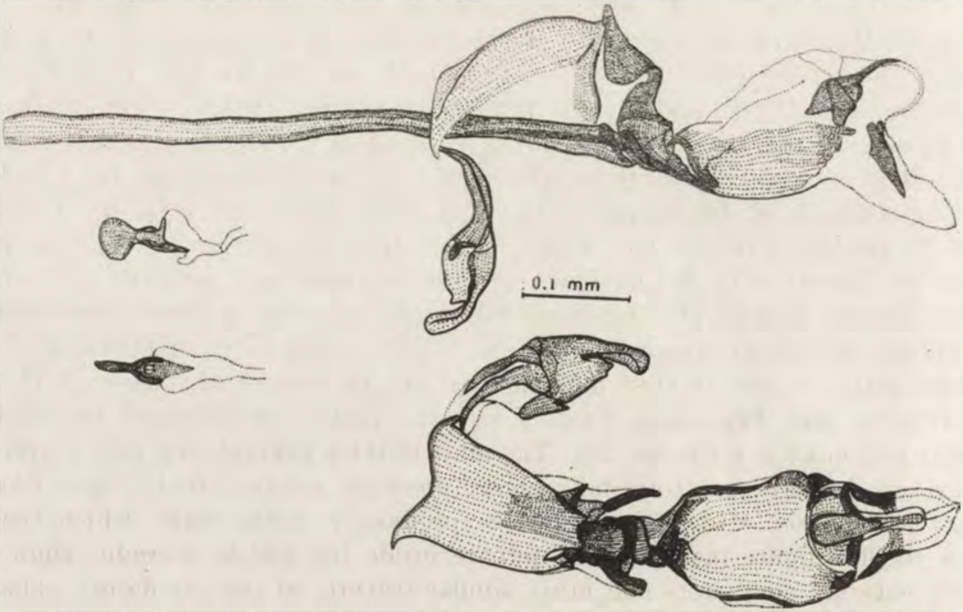


Fig. 15. Male copulatory apparatus of *Phytagromyza populi* (Kalt.) (from *Populus nigra* L., Kazuń near Warszawa, 27 X 1955, leg. J. T. Nowakowski).

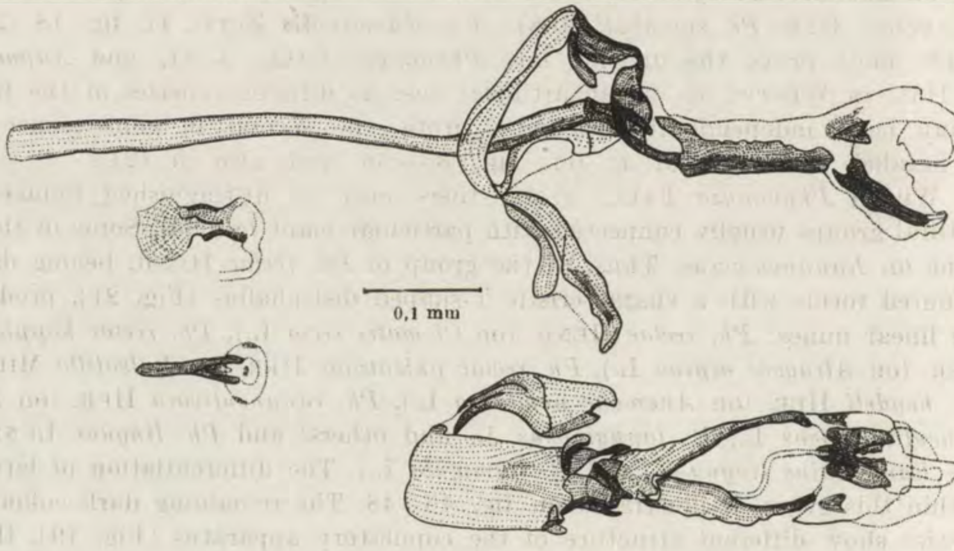
The type of the male genitalia in the natural genus *Cerodontha* Rond. is basically different from other types which are found within the artificially delimited genus *Phytagromyza* Hend., e. g. from that of the type species — *Ph. populi* (Kalt.) [Fig. 15]. The natural genus *Phytagromyza* Hend. determined by the type species seems to be limited only to the group of miners of *Salicaceae*, which comprises the following species: *Ph. populi* (Kalt.) (= *Ph. populivora* Hend.) and *Ph. populicola* (Hal.) (on *Populus nigra* L.), *Ph. tremulae* Her. (on *P. tremula* L.) and *Ph. tridentata* (Loew) (on *Salix* L.). The species feeding on the representatives of the order *Rubiales* (*Rubiaceae*, *Caprifoliaceae*, *Dipsacaceae*) form, together with many species of unknown ecology, a distinct natural genus which we name *Rubiomyza* gen. nov. designating *Phytagromyza similis* (Bri.) as its generic type.

Phytomyza FALL. s. l. certainly does not form a natural group, as it has been distinguished on the basis of the direction of curvature of the orbital hairs. The rather restricted generic value of this feature was proved when *Phytoliriomyza* HEND. and the group of *Liriomyza miki* (STROBL) were discussed (cf. pp. 86, 88). Closely related species of *Melanagromyza* HEND. also have orbital hairs bent in various directions. We shall now, however, discuss the problem of the division of *Phytomyza* FALL. s. l. into *Napomyza* HAL. in WESTW. and *Ph ytomyza* FALL. s. str. which do not differ in anything except the presence or absence of t_p. With respect to other external and genitalic characters some species groups of *Phytomyza* FALL. s. str. bear a closer resemblance to certain groups of *Napomyza* HAL. in WESTW. than to other groups of *Phytomyza* FALL. s. str. It even happens that similar species of *Napomyza* HALL. in WESTW. and *Phytomyza* FALL. s. str. are found on identical or related plants and mine in a similar way The most striking example is a pair of species living on *Lonicera* L. (*Caprifoliaceae*): *Napomyza xylostei* (KALT.) and *Phytomyza periclymeni* MEIJ. These species produce a linear mine which begins as a starlike figure (asteronome), pupate inside the leaf in a cradle, show similar external characters and fairly similar features of the copulatory apparatus [Fig. 16—17]. *Napomyza glechomae* (KALT.) living on *Glechoma hederacea* L. (*Labiatae*) is similar to dark coloured species of *Phytomyza* FALL. s. str. mining on *Labiatae*, *Boraginaceae* and *Ranunculaceae* (group of *Ph. nepetae* HEND., *Ph. petoei* HER., *Ph. symphyti* HEND., *Ph. abdominalis* ZETT., cf. fig. 18—20). These facts prove the division into *Phytomyza* FALL. s. str. and *Napomyza* HAL. in WESTW. to be an artificial one, as different species of the first group have independently originated from the second in consequence of a parallel reduction of t_p (cf. fig. 33—36 and also p. 121).

Within *Phytomyza* FALL. s. str. there may be distinguished numerous natural groups usually connected with particular plant families. Some of them mine on *Ranunculaceae*. Thus, to the group of *Ph. rectae* HEND. belong dark coloured forms with a characteristic T-shaped distiphallus [Fig. 21], producing linear mines: *Ph. rectae* HEND. (on *Clematis recta* L.), *Ph. rectae hoppiana* HER. (on *Atragene alpina* L.), *Ph. rectae pulsatillae* HER. (on *Pulsatilla* MILL.) *Ph. hendeli* HER. (on *Anemone nemorosa* L.), *Ph. ranunculivora* HER. (on *Ranunculus repens* L., *R. lanuginosus* L. and others) and *Ph. linguae* LUNDQ. (on *Ranunculus lingua* L. and *R. flammula* L.). The differentiation of larvae within this group is illustrated on fig. 45—48. The remaining dark coloured species show different structure of the copulatory apparatus [Fig. 19], they form a less close complex. In mines there may be seen a transition from a blotch mine — in *Ph. abdominalis* ZETT. (on *Hepatica* MILL.), *Ph. albimargo* HER. (on *Anemone nemorosa* L.) as well as *Ph. campanariae* NOWAK. (on *Pulsatilla* MILL.) — to a linear mine — in *Ph. calthophila* HER. and *Ph. calthivora* HEND. (on *Caltha* L.). The differentiation of the larvae in the complex is shown on fig. 41—44 and 64—65. The light coloured species belong here also to



16



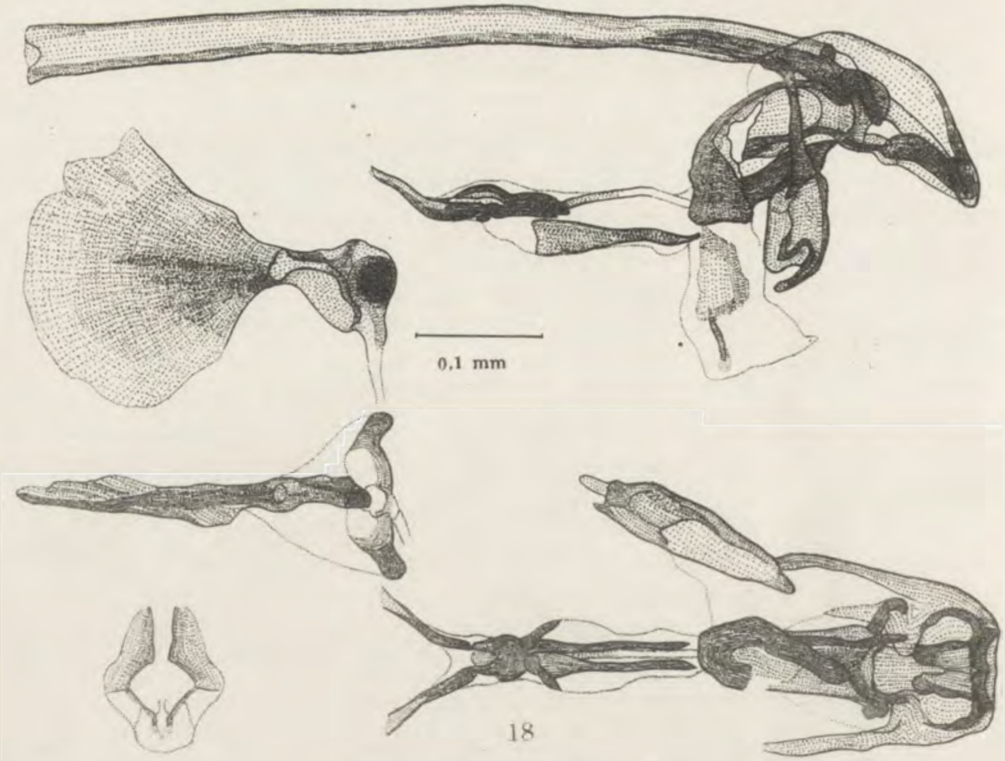
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Fig. 16—17. Artificial character of the existing division into *Napòmyza* Hal. in Westw. and *Phytomyza* Fall. s. str. Male copulatory apparatus of: 16 — *Napomyza xylostei* (Kalt.) [from *Symphoricarpus albus* (L.) Blaze, Polish Pomerania, Słupsk, 15 VIII 1925, leg. O. Karl.], 17 — *Phytomyza periclymeni* Meij. (from *Lonicera* sp., Polish Pomerania, Słupsk, 25 VII 1925, leg. O. Karl).

two unrelated groups. A linear mine and a lasso-shaped distiphallus [Fig. 22] are typical for *Ph. ranunculi* (Schr.) (on *Ranunculus* L. and *Ficaria* Adans.) as well as for *Ph. vitalbae* Kalt. (on *Clematis vitalba* L. and allied species), while an ophiogenous blotch mine and a split beak-shaped distiphallus are typical for *Ph. fallaciosa* Bri. (on *Ranunculus* L.), *Ph. anemones* Her. (on *Anemone nemorosa* L.) as well as for *Ph. hellebori* Kalt. (on *Helleborus* L.).

The dark coloured species living on *Umbelliferae* belong to the large group of *Ph. obscurella* Fall. (except the isolated *Ph. pubicornis* Hend.). The light coloured forms are included within the complex of *Ph. albiceps* Meig. Examination of the male genitalia proved the complex to be divided into two groups: one on *Umbelliferae* and one on *Compositae*. The author calls the former one the group of *Ph. angelicae* Kalt. and he distinguishes within it four subgroups. To the first subgroup belong i. a. *Ph. angelicae* Kalt. (blotch mine on *Angelica* L. and *Archangelica* Hoffm.), *Ph. pauliloewi* Hend. [blotch mine on *Peucedanum oreoselinum* (L.) Mnch. and *Pimpinella* L.] as well as *Ph. selini* Her. (linear-blotch mine on *Selinum* L.). The second subgroup includes i. a.: *Ph. pimpinellae* Hend. (broad linear mine on *Pimpinella* L.) and *Ph. chaerophylliana* Her. (linear mine on *Chaerophyllum temulum* L.). The third subgroup is represented by *Ph. heracleana* Her. (inter-parenchymal blotch mines on numerous *Umbelliferae*). Finally to the fourth subgroup producing linear mines belong: *Ph. spondylli* R. D. (on *Heracleum* L.), *Ph. pastinacae* Hend. (on *Pastinaca* L.), *Ph. sii* Her. (on *Sium* L. and *Berula* Koch), *Ph. cicutae* Hend. (on *Cicuta* L.) and *Ph. angelicastri* Her. (on *Angelica* L.). The differentiation of the larvae within the last subgroup is given on fig. 49—52, 59 and 62—63.

All the species of *Phytomyza* Fall. s. str. living on *Compositae* produce linear mines. The group of *Ph. albiceps* Meig., being divided into a series of minor ones, includes i. a. *Ph. albiceps* Meig. (on *Artemisia* L.), *Ph. matricariae* Hend. [on *Matricaria* L., *Anthemis* L., *Achillea* L. and, according to Buhr (1932, 1941, 1954), on other allied genera too], *Ph. leucanthemi* Her. (on *Chrysanthemum* L.), *Ph. tenaceti* Hend. (on *Tanacetum* L., fig. 68), *Ph. klimeschi* Her. (on *Achillea* L., fig. 69), *Ph. lappina* Gour. (on *Arctium* L.), *Ph. eupatorii* Hend. (on *Eupatorium* L.), *Ph. cirsii* Hend. (on *Cynareae*) and *Ph. sonchi* R. D. (on *Liguliflorae*) as well as *Ph. conyzae* Hend. (on *Inuleae*), with a yellow scutellum. *Ph. erigerophila* Her. (on *Erigeron* L.) is a sibling of *Ph. solidaginis* Hend. (on *Solidago* L.). To the oligophagous *Ph. affinis* Fall. (on *Cynareae*) are related not only *Ph. robustella* Hend. living presumably in stem bases of *Compositae* (Hering, 1956) and the group of *Ph. cecidonomia* Her. producing zoocecidia on leaf petioles of *Liguliflorae* (Buhr, 1955) but also *Ph. hieracii* Hend. (on *Hieracium* L.). This polymorphus species with yellow femora is a sibling of *Ph. analis* Zett. which, consequently, should be also included in the group of *Ph. affinis* Fall.



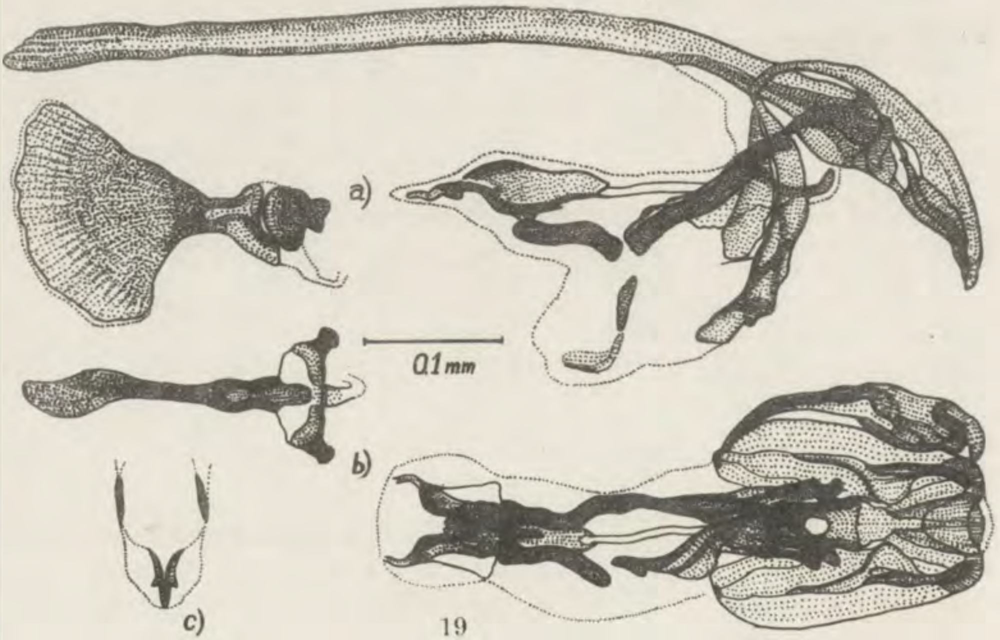


Fig. 18–19. Artificial character of the existing division into *Napomyza* Hal. in Witw. and *Phytomyza* Fall. s. str. Male copulatory apparatus of: 18 – *Napomyza glechomae* (Kalt.) (from *Glechoma hederacea* L., Polish Pomerania, Słupsk, 12 II 1925, leg. O. Karl), 19 – *Phytomyza campanariae* Nowak. [from *Pulsatilla pratensis* (L.) Mill., Kampinos Forest, Łuże, 21 VIII 1956; after Nowakowski, 1958].

Thus, we see that the classification based on genital apparatus makes necessary the division of certain large artificial genera into more numerous but smaller natural genera, i. e. groups of species usually revealing very similar biotic and ecological characters or even proving to be ecological ("biological") vicariants.

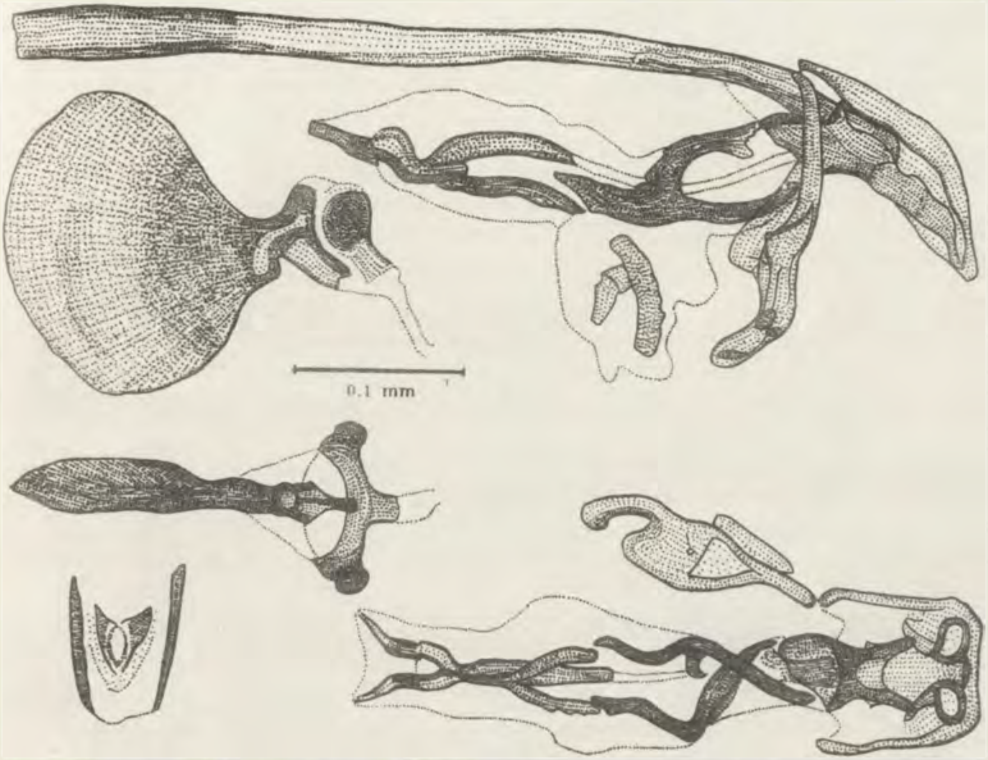


Fig. 20. Male copulatory apparatus of ***Phytomyza petoei*** HER. [from *Mentha longifolia* (L.) HUDS., Pomerania, Kashubian Switzerland, Dzierżążno, 28 VIII 1956, leg. J. T. NOWAKOWSKI].

The Female Genital Apparatus

We find in the literature a number of both general and detailed descriptions of the female genital apparatus in the *Agromyzidae* (MIALL and TAYLOR, 1907; HENDEL, 1931; SÉGUY, 1934; MELIS, 1935; VENTURI, 1936; CIAMPOLINI, 1952; SASAKAWA, 1958). SASAKAWA who has recently begun a systematic examination and description of these organs revealed remarkable differences between species and groups of species, a fact to be expected in accordance with the considerable differentiation of the male genitalia. The female genital organs may serve to distinguish and identify species and may contribute to the building of a natural system as well.

The Larva

General descriptions of the external morphology of the Agromyzid larva were given by DE MEIJERE (1925), HENDEL (1931), HENNIG (1952), FRICK (1952) and ALLEN (1957), while MIALL and TAYLOR (1907) also described the internal anatomy. Larvae of the particular species were described by DE MEIJERE (1925—1950), HERING (special papers since 1954) and recently by ALLEN (1956, 1957, 1958) who introduced a new method of examining and drawing the puparia, and by KURODA (1960). The descriptions and illustrations by VENTURI (1935, 1936, 1946) are highly valued. HENNIG (1952) compiled a commentary to the results of the investigations carried out before 1950.

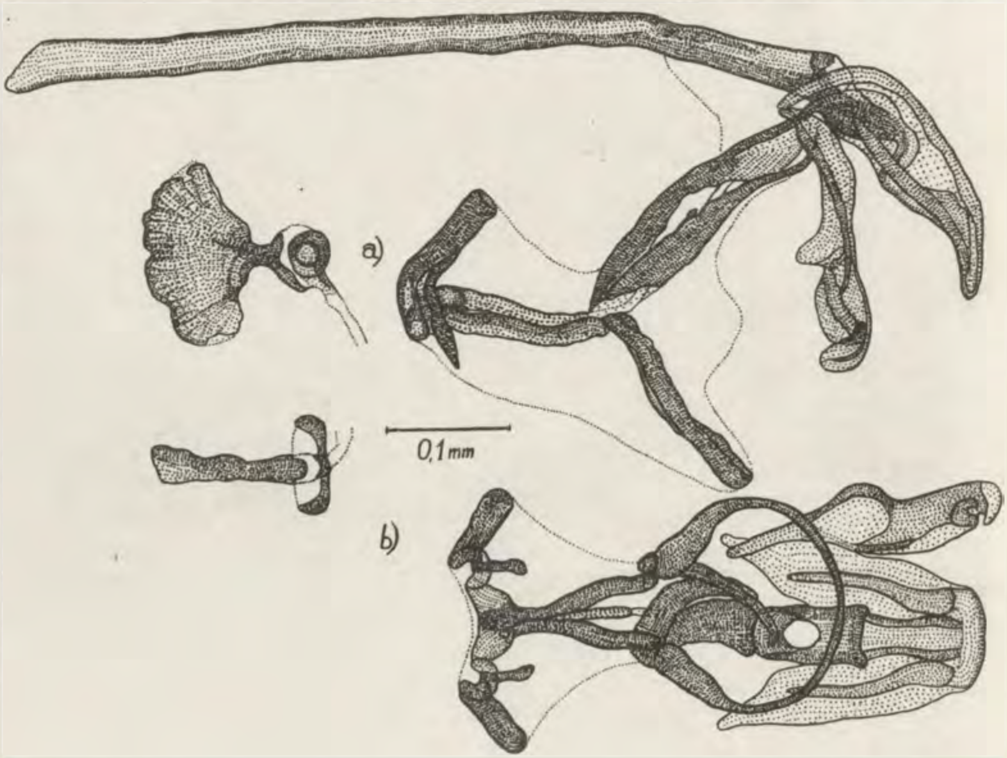


Fig. 21. Male copulatory apparatus of *Phytomyza ranunculivora* HER. (from *Ranunculus lanuginosus* L., Kampinos Forest, Reservation Sieraków, 10 X 1955; after NOWAKOWSKI, 1958).

The descriptions concern in most cases only the third (mature) larval stage, very rarely the second stage, which resembles as a rule the third. The first larval stage, on the other hand, remains hardly known till now, although it may differ considerably from the two later stages, e. g. in *Agromyza* FALL. where it seems to recapitulate certain fragments of the earlier phases of the larval phylogeny. No wonder that some species were taken in that stage for repre-

sentatives of other genera or even of an other subfamily, as it was in the case of *A. celtidis* NOWAK. (cf. NOWAKOWSKI, 1960b).

Hitherto, the larvae seemed to be far more differentiated than the adults (cf. DE MEIJERE, 1925; HERING, 1954; ALLEN, 1957). Examination of the male and female genitalia gives, however, quite an opposite picture. Poecilogony which might have seemed widespread enough with a superficial knowledge of the imagines turns usually to be alleged. Nevertheless, external and even

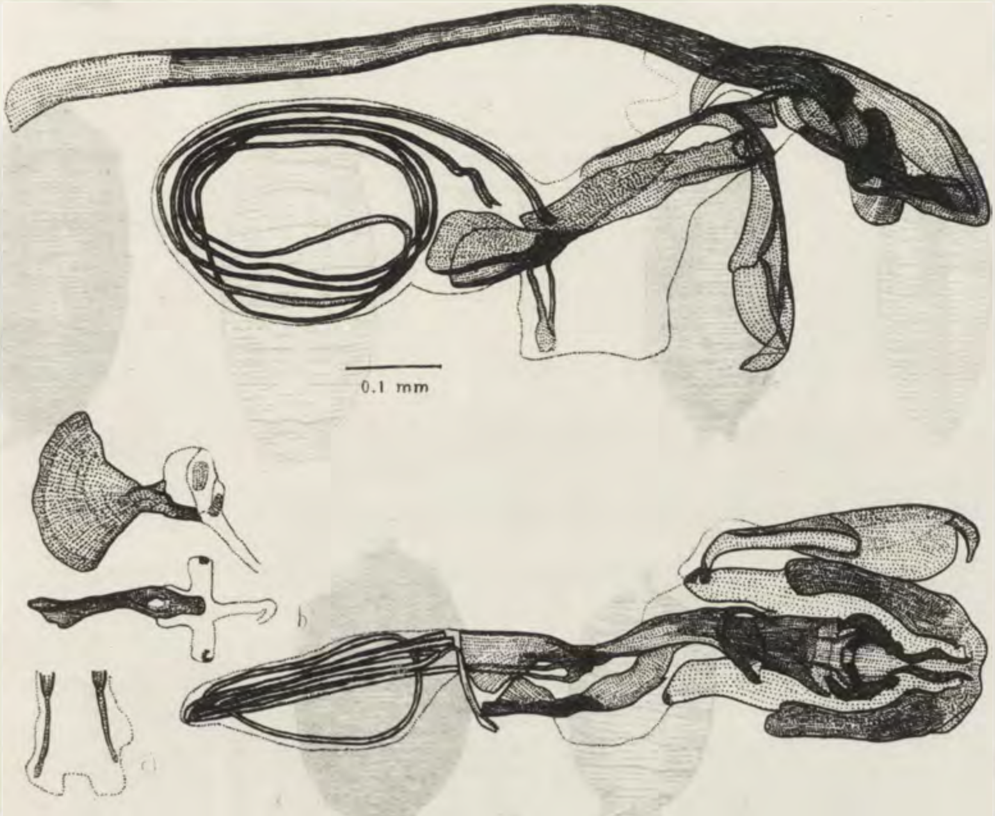


Fig. 22. Male copulatory apparatus of *Phytomyza ranunculi* (SCHRK.) (Kraków, 18 V 1886, leg. A. WAGA).

genitalic differences between the adults are sometimes so insignificant that they might escape notice, if not confronted with larval differences. This may be seen e. g. in the group of *Phytomyza rectae* HEND. where the copulatory apparatus, in spite of its complex structure [Fig. 21], is almost identical in all the species, while the morphological differentiation of the larvae is much more distinct [Fig. 45–48]. In general, however, the structure of the male copulatory apparatus is more specific than that of the larva.

The species are distinguished in the larval stage chiefly on the basis of the structure of the stigmae (spiracles). These organs, however, do not provide

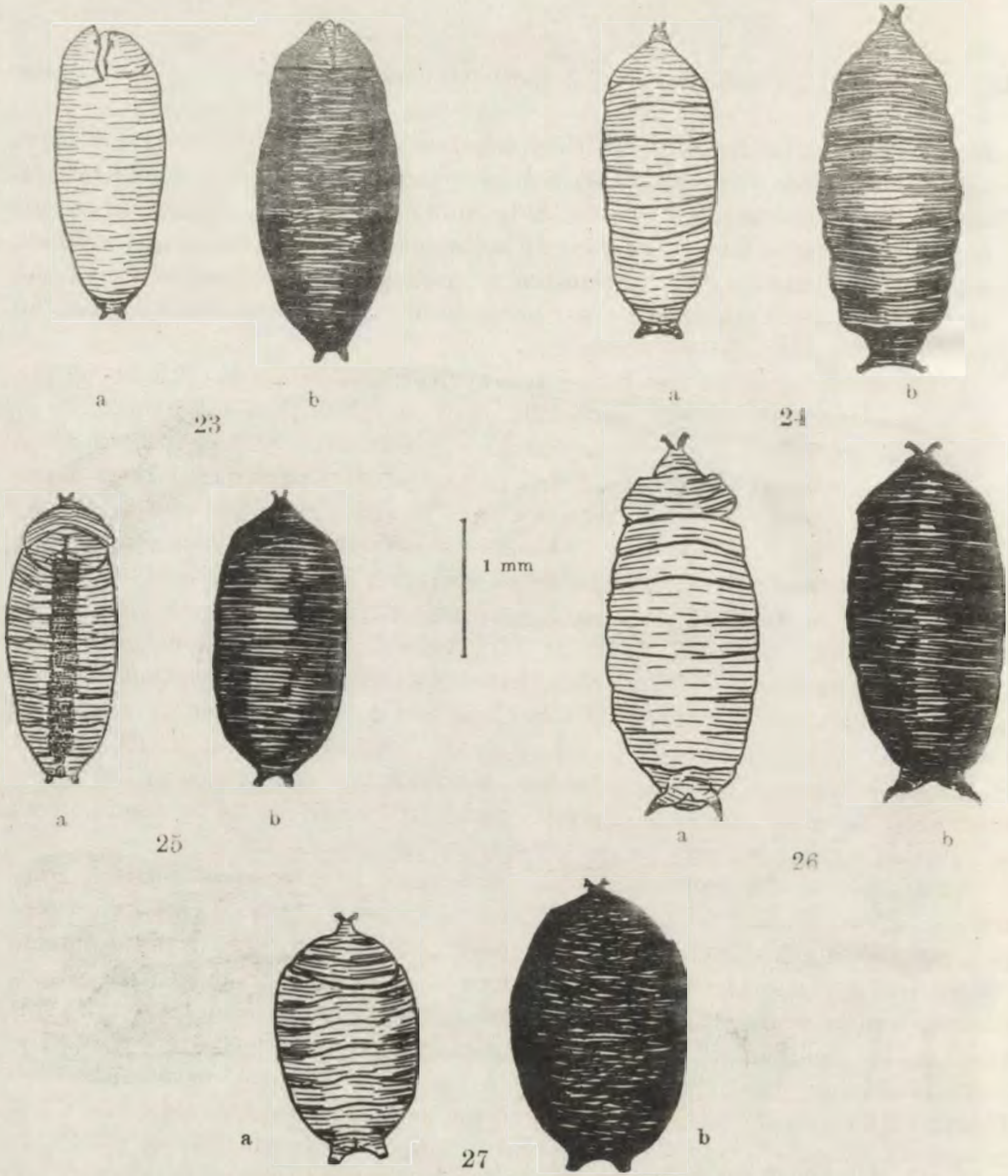


Fig. 23—27. Seasonal dimorphism of the larvae. Puparia of the non-hibernating (a) and hibernating (b) generations, in: 23 — *Ophiomyia maura* (MEIG.) (from *Solidago virgaurea* L., Kampinos Forest, a — Zamczysko, 18 VII 1955, b — Sieraków, 6 V 1956, leg. J. T. NOWAKOWSKI), 24 — *Phytomyza affinis* FALL. [a — from *Cirsium rivulare* (JACQ). ALL., Młociny at Warszawa, 10 VII 1957, b — from *Cirsium palustre* (L.) SCOP., Młociny, IV 1956, leg. J. T. NOWAKOWSKI), 25 — *Phytomyza crassiseta* ZETT. (from *Veronica chamaedrys* L. a — Kampinos Forest, Reservation Zamczysko, 20 VII 1925, b — Młociny, 29 IV 1956, leg. J. T. NOWAKOWSKI], 26 — *Phytomyza fallaciosa* BRI. (from *Ranunculus repens* L., a — Kampinos Forest, Granica, 12 VIII 1955, leg. J. T. NOWAKOWSKI, b — England, Scratch Wood, Mddx, 3 II 1956, leg. K. A. SPENCER), 27 — *Phytomyza tetrasticha* HEND. (from *Mentha aquatica* L., Kampinos Forest, Granica, a — 8 VII 1955, b — 19 III 1958, leg. J. T. NOWAKOWSKI). All the dates refer to the emergence of the imago.

valuable taxonomic features, as they are fairly variable within the species, what was stressed — probably with some exaggeration — by ALLEN (1957). The number of spiracular bulbs varies in limits exceeding $^{1}/_{3}$ of its maximum (cf. p. 125). The adaptative trend shown in the spiracles is the same for the whole family. As a result of this phylogenetic parallelism in the structure of the spiracles (cf. pp. 123—129) the larvae are generally less differentiated within the group than the copulatory apparatus.

A phenomenon which has not, till now, drawn attention is cyclomorphism, i. e. a seasonal dimorphism, consisting in a morphological differentiation of two larval generations. A dimorphism of hibernating and non-hibernating puparia was originally noted by KUWAYAMA and NISHIJIMA (1951) in a Japanese pest — *Agromyza oryzae* (MUNAKATA). The author has, till now, observed this phenomenon in 5 species: *Ophiomyia maura* (MEIG.), *Phytomyza affinis* FALL., *Ph. crassiseta* ZETT., *Ph. fallaciosa* BRI. and *Ph. tetrasticha* HEND. [Fig. 23—27]. The puparia of the two generations differ primarily in coloration: the hibernating ones being black or dark brown, the non-hibernating white, yellow or light brown. Apart from that there may occur deviations in the puparium shape and its degree of wrinkling and in the number of spiracular bulbs (in *Ph. tetrasticha* HEND., cf. NOWAKOWSKI, 1959; and in *Ph. affinis* FALL., cf. GRIFFITHS, 1959, and below). A certain correspondence in the cyclomorphism in some unrelated species seems to indicate that it results from adaptation of the autumn larval generation to hibernation.

This seasonal dimorphism has already caused a taxonomic mistake. *Phytomyza affinis* FALL. produces on *Cynareae* (except *Arctium* L.) two types of mines: an inter-parenchymal mine, yellow coloured, separated from the outside by the leaf epidermis as well as the surface layer of cells of the palisade parenchyme, and a white upper surface mine occupying the whole layer of this parenchyme and separated from the outside by the leaf epidermis only. The form producing the upper surface mine has been recently distinguished by HERING (1957a) and GRIFFITHS (1959) on the basis of larval characters as "*Phytomyza autumnalis* GRIFF." These larval differences between *Ph. affinis* FALL. and *Ph. autumnalis* GRIFF. are, in fact, differences between two larval generations of *Ph. affinis* FALL. The author found both forms of puparia, white and dark brown [Fig. 24], in both the inter-parenchymal and upper surface mines, this depending solely on the season of the year. Besides, parasitoid *Hymenoptera* do not exert any essential influence upon the coloration of the puparia of their prey. Thus, if *Ph. autumnalis* GRIFF. would be even a distinct species, its diagnosis has not been properly made up till now.

The Mine

Most of the general and detailed data concerning the leaf mines we owe to Erich Martin HERING (1926, 1951, 1935—1937, 1957), an indefatigable research worker who has conducted his studies on this subject for about 40

years. Let us add just a few short remarks on the taxonomic value of the mines.

The identification of species of mining insects according to their host plants and mines consists, in fact, in the use of the host-parasite discrimination method. A mine being the specific (i. e. peculiar for a species) feeding pattern of the larva in a definite plant organ and tissue is a visible sign of the parasite specificity. But in many cases mines of different species of insects found on the same plant are so much like one another that in order to identify their producers it is necessary to examine the larvae and puparia. It is especially difficult to identify mines in narrow leaves (*Gramineae*, *Cyperaceae*, *Juncaceae*) or in those split into tiny leaflets and lobes (*Umbelliferae*). This has many a time resulted in the repeated description of one species of miner under different names, in spite of having used the rearing method, e. g. *Cerodontha flavocingulata* (STROBL) (cf. p. 100). These difficulties have, however, to a considerable extent, been overcome in the latest key of HERING (1957a) based upon the larval morphology as well. In most cases examination of both the mine and larva makes it possible to identify the species. Nevertheless, it is sometimes difficult to notice any differences between larvae of species living together on the same plant and in such cases identification without rearing of the adult is simply impossible. Such a pair of species represent e. g. *Agromyza rufipes* MEIG. and *A. ferruginosa* WULP. on *Symphytum* L. or *Cerodontha* (*Pooemyza*) *incisa* (MEIG.) and *C.* (*P.*) *pygmaea* (MEIG.) on *Gramineae*.

The problem of intraspecific variability of the mines has not yet drawn enough attention. May the same species constantly leave different feeding patterns or, vice-versa are there any "physiological species" producing various mines but morphologically identical in all their developmental stages? When such doubts arise a thorough examination of the larval feeding habits of a species usually shows inconstancy in the differentiation of mines. E. g. after HERING (1957a) the oligophagous *Agromyza spiraeae* KALT. produces only linear-blotch mines on *Rosoideae*. Another species of *Agromyza* FALL. was supposed to be a producer of linear mines not expanding into a clear blotch. As the author has not noticed any differences either between larvae from both types of mines or between males reared from these larvae, and as on more abundant material he has found numerous transitions between the two types of mines he is inclined to suppose that the only producer of these mines is the same species — *Agromyza spiraeae* KALT. The already mentioned differentiation of the mines of *Phytomyza affinis* FALL. into inter-parenchymal and upper surface mines provides a further example of a similar kind. Larvae and puparia from these mines are identical but cyclomorphous. This was, unfortunately, used for distinguishing *Phytomyza autumnalis* GRIFF. The author has not only established, like GRIFFITHS (1959), the identity of males reared from the two differently mining larvae but also found intermediates between the two types of mines: mostly white linear mines, with certain sections coloured

yellow. It is probable that a specific mine is to some extent influenced by the host plant: on *Cirsium arvense* (L.) Scop. the author found only the inter-parenchymal mine, on *Carduus crispus* L. — only the upper surface one, while on *Cirsium palustre* (L.) Scop. and *C. oleraceum* (L.) Scop. — the upper surface mine or mines of the intermediate type. Besides, in some other species the mines are not constantly inter-parenchymal. The above mentioned intermediates are found e. g. in *Phytagromyza populi* (Kalt.) on *Populus nigra* L., in *Phytomyza farfarae* Hend. on *Tussilago farfara* L. and in *Phytomyza doronici* Her. on *Doronicum austriacum* Jacq. It must be admitted, however, that in spite of even striking morphological and ecological differences between host plants, the mines of the same species found on these plants do not reveal generally — in their external shape at least — any constant differentiation. Opposite phenomena are exceptional.

Here arises the question of the differentiation of allegedly oligophagous forms into monophagous "physiological species" attached to various host plants. Hitherto, the species of *Agromyzidae* have many a time been distinguished and described in practice on the basis of ecological or biotic peculiarities without sufficient consideration of their morphology. As the genital apparatus and often the structure of the larva have not been taken into account, the distinguishing of a species or its identification was based, on the one hand, on the host plant and the mine and, on the other, on the external morphology of the adult. As these two aspects have not always been in accordance with each other, priority of importance has been ascribed to the first. It must be stressed that this procedure was essentially correct and brought a considerably smaller number or errors than might be expected from the opposite one. It was thus proved again that ecological or biotic peculiarities are equally if not more important in taxonomy than structural ones (cf. Thorpe, 1940). But now, as we have deepened our morphological studies, let us take ecological and morphological data as being of equal value.

In distinguishing species on the basis of mines or host plants there were ascribed to these species certain morphological peculiarities which on more abundant material not always appeared to be specific. Examination of the genitalia and of the larvae provides in most cases an adequate differential diagnosis for these "mine-species", however, even taking these into account we sometimes fail to observe any structural evidence of the distinctness of these species. Hendel (1931—1936) synonymized a number of "mine-species" that had been previously described by himself or by Hering. Some of these forms the author proved to be distinct, morphologically confirmed species, e. g. *Phytomyza origani* Her. (on *Origanum* L.), *Ph. tetrasticha* Hend. (on *Mentha* L.) and *Ph. nepetae* Hend. (on *Nepeta* L.) are distinct from *Ph. obscura* Hend. (on *Satureja* L.), while *Ph. aromatici* Her. (on *Chaerophyllum aromaticum* L.) from *Ph. chaerophylli* Kalt. (on *Chaerophyllum bulbosum* L.). Yet *Ph. aromatici* Her. does not differ clearly not only from a form living on *Chaerophyllum te-*

mulum L. but also from *Ph. anthrisci* HEND. (on *Anthriscus* PERS.) and *Ph. tordylli* HEND. (on *Torilis* ADANS.). These three forms could claim to be called "physiological species". LUNDQUIST (1949) described two species on *Ranunculus lingua* L., namely *Phytomyza linguae* LUNDQ. and *Ph. ranunculiphaga* LUNDQ., without giving any sufficient morphological basis for their specific distinctness from corresponding forms living on *Ranunculus acer.* L., *R. repens* L., *R. lanuginosus* L. etc. Examination of the larvae and genitalia made by the author has proved *Ph. linguae* LUNDQ. to be, in fact, distinct from *Ph. ranunculivora* HER. [Fig. 47—48], but there is still lacking any clear morphological evidence for the distinctness of *Ph. ranunculiphaga* LUNDQ. from *Ph. fallaciosa* BRI.

According to MAYR (1942) it is not surprising that reproductive isolation very often does not involve constant structural differentiation. It seems to be probable, however, that such may be the case only in incipient species or those more recently originated. Occurrence of some individuals on even completely different hosts does not give in itself any proof of their specific distinctness, nor does it the intuition of a taxonomist. Wherever simple descriptive and comparative methods fail to provide a clear diagnosis better results could be expected after the use of biometric methods, rearing and transplantation experiments and cytogenetic investigations.

Evolutionary Trends

When certain complexes of characters evolve in the same direction in various groups of common origin we are faced then with both orthoevolution[1] and phylogenetic parallelism. These both result in independent appearance of similar but not directly related forms representing some common evolutionary phase or stage. By uniting these forms in taxonomic units, polyphyletic groups, so-called "stage groups" (Stadiengruppen; REMANE, 1952) become established. As evolution often consists in the reduction of certain structures or organs, certain "stage groups" are, at the same time, "negative groups" (Negativgruppen; REMANE, 1952) distinguished by the lack of a certain feature.

Phylogenetic parallelism cannot be strictly distinguished from convergence — neither in theory, nor in practice. Convergence in its strict sense means resemblance of analogous organs of unrelated organisms, caused by their adaptation to the same environment or function, whereas parallelism — independently evolved resemblance of homologous organs of organisms which are related

[1] The term "orthoevolution" (PLATE, 1913) is accepted here as with the term "orthogenesis" various and extreme interpretations of directional (rectilinear) evolution are connected.

but undirectly, i. e. homoiology (PLATE, 1928; cf. HENNIG, 1950). REMANE (1952) who in fact identifies homology with relationship considers homoiology as a sort of analogy. HENNIG (1953), on the other hand, considering convergence in a broader sense, includes homoiology in it. Thus, homoiology (or phylogenetic parallelism) should be considered as some combination of homology in its strict sense (or phylogenetic relationship) and analogy in its strict sense (or convergence).

Directional evolution is rarely a fully rectilinear one, usually it consists only in the dominance of some evolutionary trend over tendencies directed otherwise which, however, may at times be prevailing, thus causing the reversibility of evolution of particular characters. That is why realization of some trends in evolution does not contradict its mosaic pattern.

In the *Agromyzidae* directional and parallel evolution includes complexes of characters similar to those in certain other groups of *Diptera*, and even in certain other groups of insects: general size of body, wing venation, chaetotaxy and larval spiracles. HENDEL (1936), DE MEIJERE (1950) and FRICK (1952) have occasionally noticed some of these facts but it was not till the examination of genital apparatus and the establishment of vertical divisions of the group that a better understanding of the evolutionary trends was made possible.

In the evolution of insects decrease of the body size is prevailing in connection with their flight mechanics and trachaeal respiring. In the *Agromyzidae* this evolutionary trend possesses a clearly adaptative character mainly because of the small body size being more suitable for larvae mining in thin leaf blades. Thus, HARRISON's parasitological rule (cf. OSCHE, 1958) applies to these endophagous insects, with but one correction, i. e. the size of the parasite being not correlated with the whole body size of the host but with the size of its invaded organ, or even rather with the thickness of the layer of the tissue used as food by the parasite. Agromyzid species feeding in the cambium, stem pith, stem bases and inflorescences are usually bigger than those mining in leaves, in the latter case an influence of the thickness of the leaf blade and of its surface upon the size of the insect is noted. However, even when these influences are eliminated it can be seen that plesiomorphous forms are in most cases bigger than apomorphous ones. E. g. within the genus *Agromyza* FALL. the species: *A. reptans* FALL., *A. rufipes* MEIG. or the group of *A. ambigua* FALL. surpass in size most representatives of the groups of *A. cinerascens* MACQ., *A. nana* MEIG. and *A. spiraeae* KALT. Representatives of *Dendromyza* HEND., and *Nemorimyza* FREY are usually bigger than those of *Trilobomyza* HEND., *Praspedomyza* HEND. and *Calycomyza* HEND. Within *Calycomyza* HEND. the most plesiomorphous *C. artemisiae* (KALT.) is bigger than *C. humeralis* (V. ROS.) and *C. solidaginis* (KALT.). *Encoelocera* LOEW showing the largest body size among the *Agromyzidae* is a plesiomorphous genus of unknown ecology, but no leaf miner in any case. From among the representa-

4

tives of the apomorphous genus *Phytomyza* Fall. s. l. only species of unknown ecology, such as *Napomyza elegans* (Meig.), *Phytomyza nigripennis* Fall. and *Ph. robustella* Hend. reach the size of the largest plesiomorphous forms. Genera of a markedly dwarfed size, i. e. *Haplomyza* Hend., *Irenomyia* Nowak., *Xeniomyza* Her. in Meij. and especially *Ptochomyza* Her. manifest a number of other apomorphous characters too.

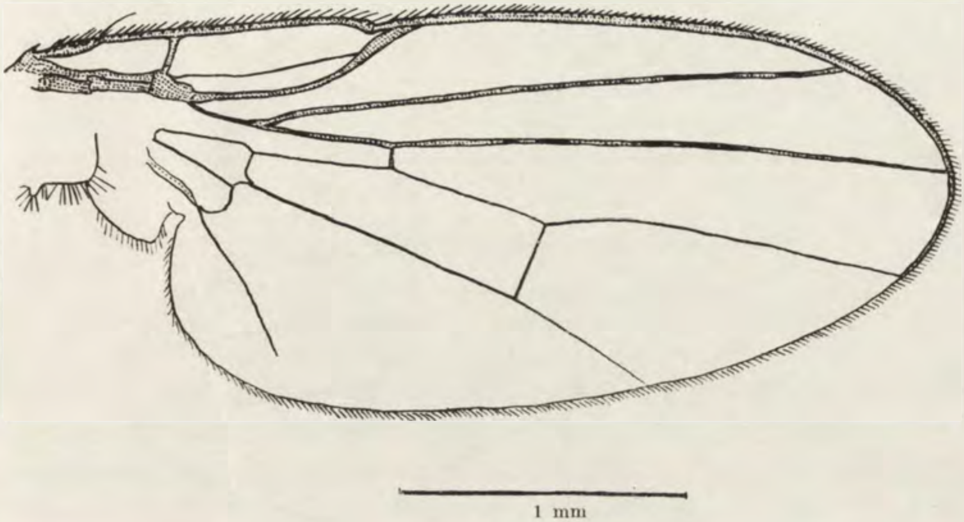
Directional and parallel evolution of wing venation is manifested here in the costalization, i. e. costal concentration (Rohdendorf, 1946; cf. Švanvič, 1949). The process consists here in shifting of the anterior longitudinal veins towards the anterior margin of the wing, and in shortening of the costa to the anterior margin of the wing, with simultaneous proximal translocation of both transverse veins, reduction of the posterior transverse vein, and thinning out or even partial reduction of the posterior longitudinal veins.

The shifting of the anterior longitudinal veins towards the anterior margin of the wing is connected with shifting of their distal ends forward and then to the basis of the wing. The position of the ends of m_{1+2} and r_{4+5} on both sides of the wing apex must be considered as plesiomorphous. In most representatives of the subfamily *Agromyzinae* the and of r_{4+5} is nearer to the apex of the wing than the end of m_{1+2} [Fig. 28–29], in most of the *Phytomyzinae* a reciprocal relation [Fig. 30–32] is observed. However, in the group of *Agromyza rubi* Bri. (= *A. sulfuriceps* Strobl) there has already taken place the shifting typical for the *Phytomyzinae*, while *Phytobia* Lioy (= *Dendromzya* Hend.) and *Nemorimyza* Frey, as well as some representatives of *Rubiomyza* gen. nov., had stopped in this respect at the stage of the subfamily *Agromyzinae*.

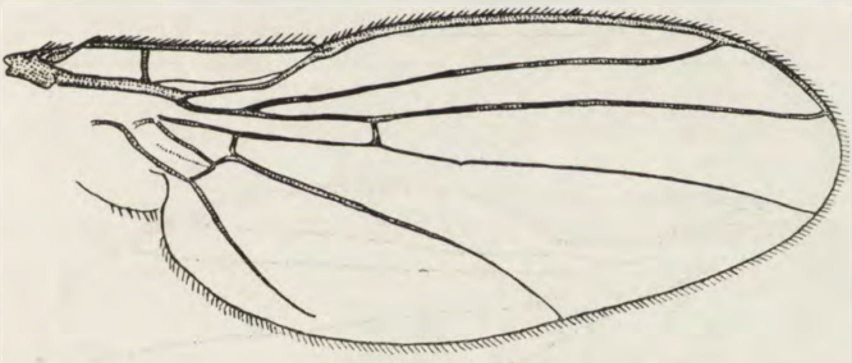
When the end of m_{1+2} extends to the apex of the wing and, thus, the vein takes a position on the longitudinal axis of the wing its further shifting depends on whether it keeps a connection with the end of the contracting costal vein. Thus, there are two ways in which costalization may take place. If the terminal section of the costa between the end of r_{4+5} and that of m_{1+2} does not disappear, the end of m_{1+2} may translocate before the apex of the wing and shift further towards its basis as if pulled by the end of the contracting costa. Then m_{1+2} does not get thinner but shifts forward following both branches of the radial sector, i. e. the veins r_{2+3} and r_{4+5}. As a result there follows the full costal concentration of the longitudinal veins. If, however, the terminal section of the costa disappears and thus m_{1+2} is torn off from the costa, m_{1+2} stops on the longitudinal axis of the wing and gets thinner, just as the posterior longitudinal veins: m_{3+4} and *an* do.

Various stages of costalization of the first type may be observed in: *Campanulomyza gyrans* (Fall.), in certain species of *Liriomyza* Mik, in *Metopomyza* Enderl., *Haplomyza* Hend., *Irenomyia* Nowak. [Fig. 38] and *Xeniomyza* Her. in Meij. [Fig. 39]. Hendel (1931) failed to notice that the end of m_{1+2} had already shifted before the wing apex in at least five Palaearctic representatives of *Liriomyza* Mik, i. e. in *L. cicerina* Rond., *L. artemisicola*

MEIJ., *L. haploneura* HEND., *L. deficiens* HEND. and *L. latigenis* (HEND.); the three latter species, because of the simultaneous lack of t_p and a scanty number of orbital hairs, should be included into *Haplomyza* HEND. sensu MELANDER. Thus, the genus in question occurs also in the Palaearctic. The author was unable, however, to check whether this genus represents a natural group (cf. NOWAKOWSKI, 1960a).



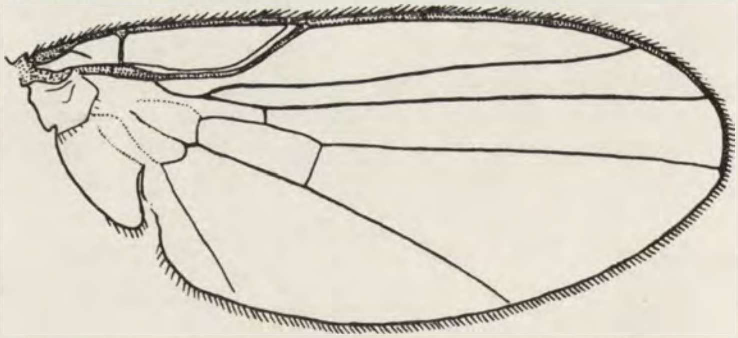
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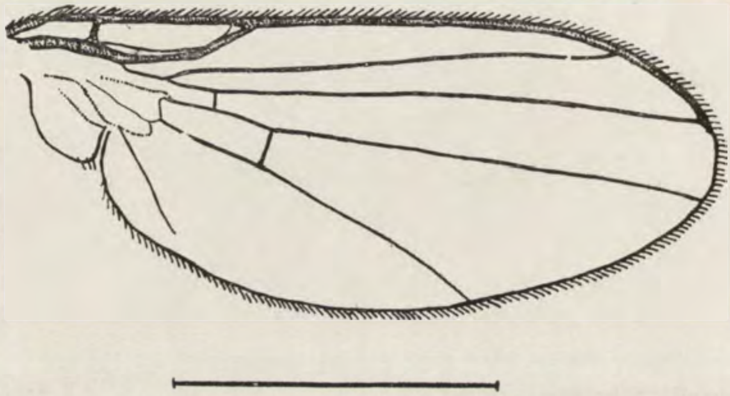
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Fig. 28—29. Reduction of the terminal section of the costa and of t_p in *Agromyza* FALL. Wing of: 28 — *Agromyza reptans* FALL., 29 — *A. intermittens* BECK.

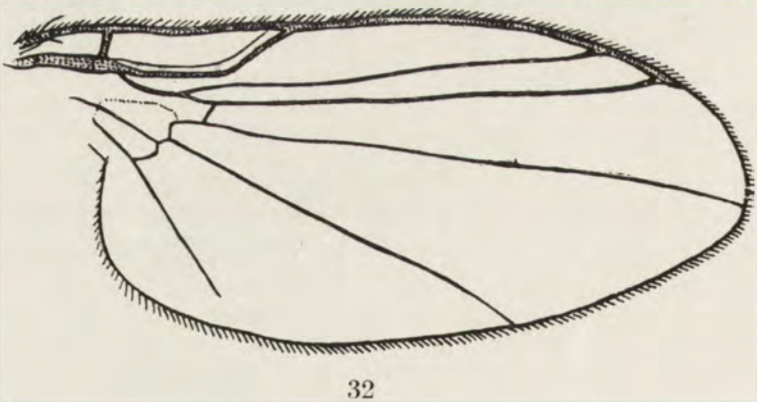
Costalization of the second type is connected — as it has already been mentioned — with atrophy of the terminal section of the costa between the ends of m_{1+2} and r_{4+5}. We observe this reduction in statu nascendi, e. g. within three genera of *Agromyzinae*: *Agromyza* FALL. [Fig. 29], *Melanagromyza* HEND. and *Ophiomyia* BRASCHN. In case when the terminal section of the costa is



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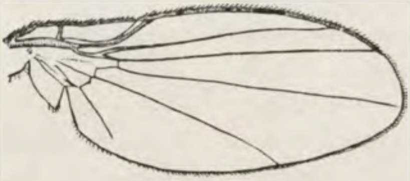
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Fig. 30–32. Reduction of the terminal section of the costa and of t_p. Horizontal division into *Phytobia* Lioy s. l. and *Phytagromyza* Hend. Wing of: 30 – *Pooemyza incisa* (Meig.), 31 – *Phytagromyza flavocingulata* (Strobl), 32 – *Phytagromyza populi* (Kalt.).

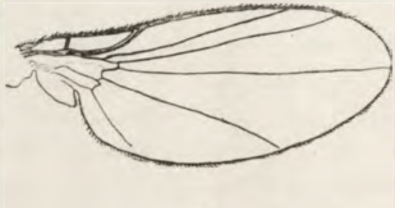
still preserved it undergoes gradual but distinct atrophy: it contracts or gets thinner with the effect that sometimes it is hard to notice and causes misidentifications. The representatives of *Agromyza* FALL. in which the terminal section of the costa was atrophied had previously been united in a horizontal genus *Domomyza* ROND. which was a typical "negative group" (cf. pp. 97–98). In the subfamily *Phytomyzinae* the reduction of the terminal section of the costa proceeds also independenly in a number of phyletic lines. At the ends of these lines are: *Amauromyza madrilena* SPENC. and *Cerodontha* (*Xenophytomyza*) *atronitens* (HEND.) in which the costa ends at half the distance between r_{4+5} and m_{1+2}, *Cerodontha flavocingulata* (STROBL) [Fig. 31], *Phytobia laticeps* (HEND.) and *Ph. lunulata* (HEND.), the two last species distinguished by ENDERLEIN (1936) as a separate genus *Liomyzina* ENDERL., further the genera *Phytagromyza* HEND. [Fig. 32], *Rubiomyza* gen. nov., *Pseudonapomyza* HEND., and *Phytomyza* FALL. s. l. [Fig. 33–37]. In many species the costa extends still further behind the end of r_{4+5} and the trace of its former course may be seen. When m_{1+2} takes a position on the longitudinal axis of the wing, then it stops there and only both the branches of the radial sector shift forward. The degree of their shifting varies here even intraspecifically and therefore it is hardly possible to use HENDEL's key which separates larger species groups of *Phytomyza* FALL. s. str. according to the ratio of the costal sections contained between the ends of r_1 and r_{2+3} and of r_{4+5} and m_{1+2}.

The shifting of the anterior longitudinal veins results in opening the angle between m_{3+4} and m_{1+2}, and (in costalization of the second type) between m_{1+2} and r_{4+5} too. This makes the posterior (t_p, i. e. $m-m$) and anterior (t_a, i. e. $r-m$) transverse veins to move towards the basis of the wing and causes reduction of t_p. Proximal translocation or atrophy of t_p makes it possible for m_{1+2} to be torn off from m_{3+4} and for its shifting forward, while atrophy of the terminal section of the costa and proximal shifting of t_a makes it possible for r_{4+5} to be torn off from m_{1+2}. Shifting of t_p and t_a in the proximal direction may be traced already in *Calycomyza* HEND. and partly in *Liriomyza* MIK, including *Cephalomyza* HEND. and *Praspedomyza* HEND., it occurs more distinctly in many representatives of *Phytagromyza* HEND. and *Rubiomyza* gen. nov. and in *Napomyza* HAL. in WESTW. [Fig. 33, 35, 37]. The location of t_p and thus the ratio of the sections of vein m_{3+4} varies considerably within many species, e. g. in *Agromyza flavipennis* HEND., *Cerodontha flavocingulata* (STROBL), *Cerodontha* (*Pooemyza*) *lateralis* (MACQ.), *C.* (*Pooemyza*) *morula* HEND., *Liriomyza sonchi* HEND., *Liriomyza bryoniae* (KALT.). It is one more reason why it cannot be used as diagnostic of genera. Due to the variability of this feature *Cerodontha flavocingulata* (STROBL) has recently been described repeatedly under new names, as *Phytagromyza spinicauda* HEND. (t_p close to t_a) and as *Ph. ensifera* HER. (t_p far from t_a, cf. p. 100). In certain representatives of *Napomyza* HAL. in WESTW. t_p has already shifted on to the prolongation of t_a [in *N. annulipes* (MEIG.) and *N. hirticornis* HEND.] or even into a proximal position in relation

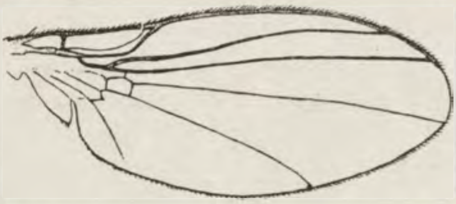
to t_a [in *N. elegans* (MEIG.), Fig. 37, *N. lateralis* (FALL.) and *N. nigriceps* (WULP.)]. In *Phytomyza* FALL. s. str. [Fig. 34, 36] t_p has disappeared, while t_a has shifted close to the base of the wing. Anomalies consisting in the appearance of additional transverse veins distally or proximally from t_a or t_p, could be treated as expressing some tendency towards shifting of transverse veins or as traces of this evolutionary process. These anomalies were observed by HENDEL (1931) in *Cerodontha* (*Dizygomyza*) *bulbiseta* (HEND.), by HERING



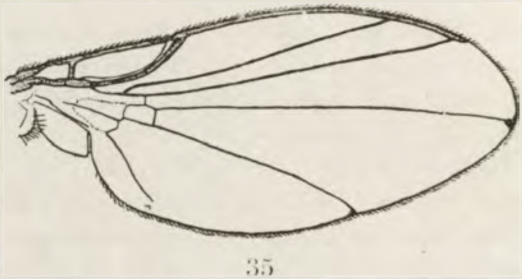
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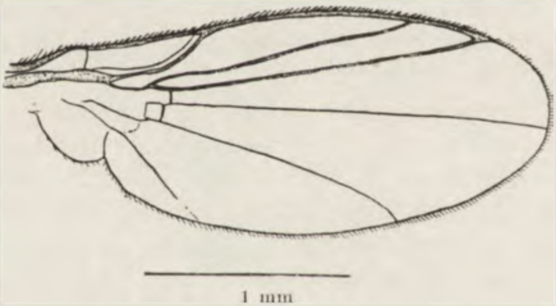
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Fig. 33—37. Proximal translocation and reduction of t_p in *Phytomyza* FALL. s. l. Horizontal division into *Napomyza* HAL. in WESTW. and *Phytomyza* FALL. s. str. Wing of: 33 — *Napomyza xylostei* (KALT.), 34 — *Phytomyza periclymeni* MEIJ., 35 — *Napomyza glechomae* (KALT.), 36 — *Phytomyza campanariae* NOWAK., 37 — *Napomyza elegans* (MEIG.).

(1935) in *Agromyza alnibetulae* HEND., *A. vicifoliae* HER., *Melanagromyza lappae* (LOEW), *Tylomyza pinguis* (FALL.) and *Cerodontha* (*Dizygomyza*) *bimaculata* (MEIG.), and by the author in *C.* (*D.*) *luctuosa* (MEIG.) (an additional transverse vein distally from t_a in both wings of a ♀ reared from *Carex* sp. on 15 XII 1952, mines found in Kranichsteig in Germany by F. GROSCHKE),

C. affinis (FALL.) (additional t_a in a ♂ from HENDEL's collection) and *Agromyza igniceps* HEND. (cf. NOWAKOWSKI, 1960b).

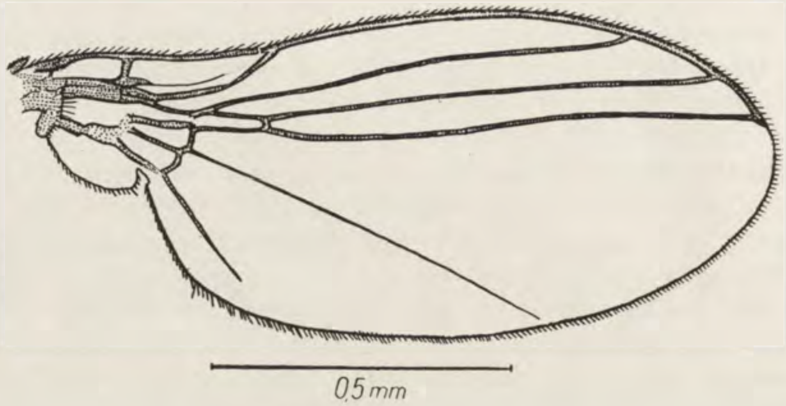
Reduction of the posterior transverse vein (t_p) is noticed in various genera and species, presence or absence of the vein being a variable character in *Agromyza intermittens* BECK. [Fig. 29]. t_p ultimately disappeared in *Ophiomyia aeneonitens* (STROBL), *Metopomyza xanthaspis* (LOEW), *Cerodontha* (*Xenophytomyza*) *atronitens* (HEND.), *Liriomyza esulae* HEND., *Haplomyza* HEND. [including *Liriomyza deficiens* HEND., *L. haploneura* HEND, and *L. latigenis* (HEND.)], *Irenomyia* NOWAK. [Fig. 38], *Xeniomyza* HER. in MEIJ. [Fig. 39], *Gymnophytomyza* HEND., *Phytagromyza* HEND. [Fig. 32], *Pseudonapomyza* HEND., in eight species of *Rubiomyza* gen. nov. and in all representatives of the "negative group" — *Phytomyza* FALL. s. str. [Fig. 34, 36]. Anomalies consisting in partial or complete reduction of t_p, in one or both wings, have been observed by HERING [1935] in *Agromyza niveipennis* ZETT., *Liriomyza cicerina* (ROND.) and *L. strigata* (MEIG.), and by the author in *Trilobomyza verbasci* (BCHÉ) (in the right wing of a ♀ reared on 1 IX 1928 from *Verbascum* spec., mine found at Rostock in Mecklenburg by H. BUHR), *Cerodontha* (*Pooemyza*) *pygmaea* (MEIG.) (partial reduction in the left wing of a ♂ collected at Helsinki by R. FREY), *C. affinis* (FALL.) (in the left wing of a specimen without abdomen, collected in Silesia in the XIX century by H. SCHOLTZ), *C. fulvipes* (MEIG.) (partial reduction in the right wing of a ♀ from HENDEL's collection), *C. flavocingulata* (STROBL) (partial reduction in the right wing of a ♂ from HENDEL's collection, identified by him as "*Phytagromyza spinicauda* HEND."), *Liriomyza flaveola* (FALL.) (partial reduction in the left wing and complete reduction in the right wing of a ♀ from HENDEL's collection) and *Napomyza salviae* HER. (complete reduction in both wings of a ♀ reared from *Salvia verticillata* L. on 29 VII 1959, mine found at Sarajevo in Yougoslavia by the author). *Napomyza ballotae* (HER.) and *N. soldanellae* (STARÝ) were originally described as representatives of *Phytomyza* FALL. s. str. probably because their types were abnormal specimens in which t_p was atrophied. "*Phytomyza secalina* HER." was described on some specimens of *Agromyza intermittens* BECK. lacking t_p (cf. HERING, 1935).

As to the reduction of the posterior longitudinal veins it is more distinct only in *Xeniomyza* HER. in MEIJ. where the anal vein has been atrophied [Fig. 39].

The reduction of wing venation seems to be caused by the decrease of the wing size and also by the costalization. Costalization represents a dominating trend in the evolution of wing venation in a number of groups of *Diptera* but it is in the family *Agromyzidae* that the process is particulary evident. ROHDENDORF (1951) distinguished even an agromyzoid subtype of wing venation as a progressive variety of the muscoid type, characterized by the more advanced costal concentration of the veins. According to ROHDENDORF costalization makes the flight organ more efficient, flight playing an important role

in *Agromyzidae*, as monophagous insects having not too strongly developed iegs and bound to seek their host plants.

In the *Agromyzidae* certain sets of bristles covering the body of the adult lnsect undergo parallel reduction. A partial atrophy of the bristles may be illustrated by the example of certain mesonotal bristles, namely the dorso-



38



39

Fig. 38–39. Costal concentration of the wing venation. Wing of: 38 — *Irenomyia obscura* (Rohd.-Holm.), 39 — *Xeniomyza ilicitensis* Her. in Meij. (after Nowakowski, 1960a).

centrals (*dc*) and acrostichals (*acr*), these being currently used in taxonomy. Plesiomorphous forms have four pairs of long *dc* behind the transverse mesonotal suture and one or more pairs of shortened *dc* before the suture. The pattern 4+1 (2, 3) has to be applied to numerous representatives of *Agromyza* Fall., to *Rubiomyza falleni* (Ryd.), *R. hamata* (Hend.) and *R. similis* (Bri.). In most of the remaining species the number of *dc* is established as 3+1. Further reduction results in patterns: 3+0 [group of *Agromyza rubi* Bri., *A. celtidis* Nowak. (cf. Nowakowski, 1960b), certain representatives of *Melanagromyza* Hend. and *Ophiomyia* Braschn., *Tylomyza madizina* (Hend.), *Amauromyza*

lamii (KALT.), *Cerodontha* (*Pooemyza*) *lateralis* (MACQ.), *Calycomyza* HEND., *Campanulomyza* gen. nov., *Rubiomyza zernyi* (HEND.), *Pseudonapomyza* HEND.], later 2+1 (*Agromyza flaviceps* FALL.) and finally 2+0 [the remaining representatives of *Melanagromyza* HEND. and *Ophiomyia* BRASCHN., *Tylomyza pinguis* (FALL.), *Irenomyia obscura* (ROHD.-HOLM.), *Metopomyza xanthaspis* (LOEW), *Encoelocera bicolor* LOEW, *Rubiomyza orphana* (HEND.), *R. buhri* (MEIJ.)]. Dorsocentral bristles when shortened become similar to *acr* so that the number of *dc* is variable or controversial within a given species [e. g. in the group of *Agromyza rubi* BRI. or of *A. ambigua* FALL., and in *Cerodontha* (*Pooemyza*) *atra* (MEIG.) and *C.* (*P.*) *deschampsiae* (SPENC.)], and that is why it cannot be, all the more, diagnostic of natural genera. Thus, e. g. the subgenus *Calycomyza* HEND. distinguished according to the pattern 3+0 was an artificial group (cf. p. 97). Similarly the key division ot the genus *Agromyza* FALL. into two groups according to the number and arrangement of *dc* (HENDEL, 1931) proved to be an artificial one.

In plesiomorphous forms the acrostichal hairs (*acr*) are arranged in 8–10 dense rows, extending far anteriorly and posteriorly, e. g. in *Agromyza rufipes* MEIG., *Encoelocera bicolor* LOEW, *Phytobia* LIOY (= *Dendromyza* HEND.). The number of rows undergoes gradual reduction, alongside with their shortening and decrease of density, to 6, 4 and 2 or even 0 [the latter e. g. in *Liriomyza* (*Cephalomyza*) *cruciferícola* (HER.), *Phytomyza atricornis* MEIG.]. The number of *acr* rows, their density and extension is of rather small taxonomic value even for distinguishing of species. The same holds true for interalar hairs (*ia*).

Reduction of bristles, apparently caused by the decrease in general body size may be assumed to be an example of quantitative reduction of homotypic parts, i. e. of oligomerization in its broader sense (DOGIEL, 1954). Aside from the dominant reduction (oligomerization), there often occurs, however, a secondary increase in the number of bristles (polymerization) (cf. HENNIG, 1958).

Parallel orthoevolution of larval spiracles is characteristic to the whole tribe *Cyclorrhapha* (HENNIG, 1950). The secondary larval stigma (spiracle; cf. DE MEIJERE, 1895) is placed upon a cuticular process (Stigmenträger). The primary (original) spiracular aperture, i. e. the tracheal opening, has sunk below the body surface and thus a cavity between the primary and secondary spiracular openings, called the atrium (Filzkammer), has developed. The secondary opening became divided into few crevices which subsequently may become divided into a number of minute spiracular pores (Tüpfel). These crevices and pores become placed upon bud processes called bulbs (Knospen). The plesiomorphous number of secondary spiracular openings of the cyclorrhaphous amphipneustic larva may be considered to be 5 pores for the anterior spiracle, and 3 crevices for the posterior one. These numbers increase, while crevices become changed or divided into pores. The atrium grows and ramifies simultaneously assuming the shape of a fan or tree (cf. de MEIJERE, 1895; HENNIG, 1950).

The plesiomorphous number of spiracular bulbs [cf. fig. 40] may still be found in numerous representatives of the *Agromyzidae*. The parallel increase of the number of spiracular bulbs is observed in various groups of the family, this amounting in the anterior spiracle finally to 50 (in the Javanese *Melanagromyza sojae* Zechntn.; cf. de Meijere, 1938) and to over 100 in the posterior one (in *Phytomyza calthivora* Hend.). The posterior spiracles will be here dealt with in detail as they are currently used for taxonomic purposes.

In the genus *Agromyza* Fall. the plesiomorphous type of the posterior spiracle bearing three crevices is still the dominating one. Larger numbers of crevices are found only in *A. rubi* Bri. (6) and *A. salicina* Hend. (8—10),



Fig. 40. Plesiomorphous number of bulbs in larval spiracles of *Irenomyia obscura* (Rohd.-Holm.): a — anterior spiracle, b — posterior spiracle (from *Caragana arborescens* Lam., Łomianki near Warszawa, 22 VI 1957, after Nowakowski, 1960a, modified).

while *A. lathyri* Hend. and *A. dipsaci* Hend. bear about 40 pores. In *Japanagromyza duchesnae* Sasak. 10 bulbs are present, in *J. quercus* (Sasak.) — 48 bulbs on three branches of the spiracle (Sasakawa, 1954).

De Meijere (1937, 1938, 1950) arranged the species of *Melanagromyza* Hend. and *Ophiomyia* Braschn. according to the number of openings on the posterior spiracle increasing from 3 crevices to 19 pores. In *Ophiomyia ranunculicaulis* Her. there are over 25 bulbs, in the Javanese *Melanagromyza ricini* Meij. — even 50.

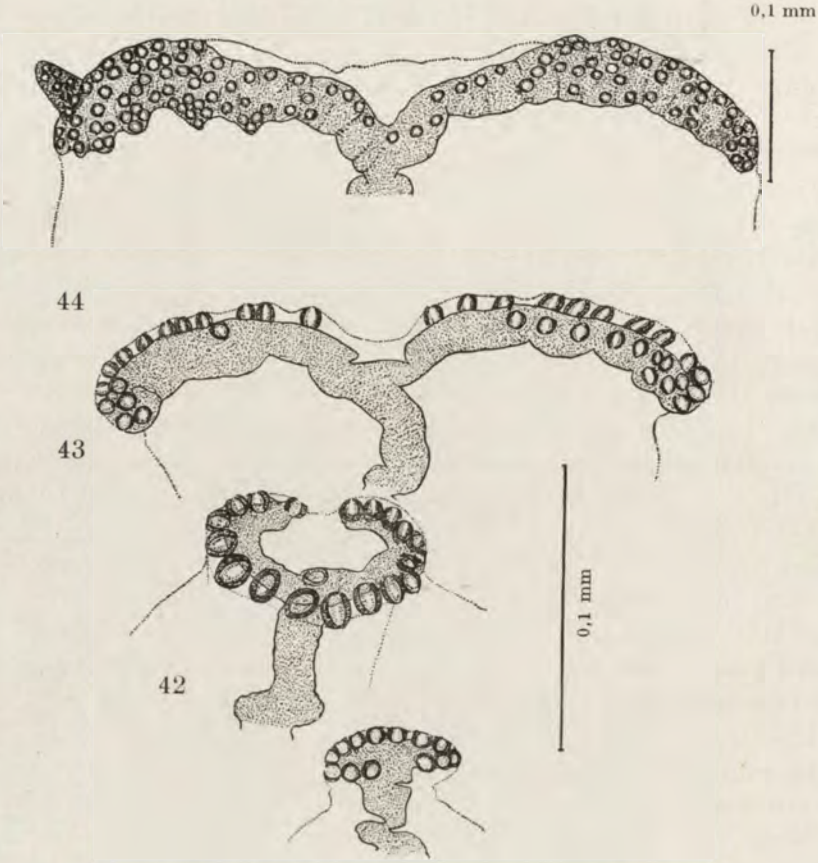
The spiracle bears three crevices in *Phytobia* Lioy, *Nemorimyza* Frey, *Trilobomyza* Hend., *Amauromyza* Hend., *Phytagromyza mamonovi* Her. and in numerous species of *Liriomyza* Mik, including *Cephalomyza crucifericola* Her. Most representatives of the complex of *Liriomyza pusilla* (Meig.) — bear about 10 bulbs, while in *L.* (*Praspedomyza*) *morio* (Bri.) 13 bulbs occur, in *L.* (*P.*) *approximata* (Hend.) — about 20. *Liriomyza* (*Cephalomyza*) *cepae* (Her.) includes three sibling species treated so far as races that differ in the number of bulbs, this being 9, 15 or 25 (Nietzke, 1943; Hering, 1956b, 1957b). *Pteridomyza hilarella* (Zett.) bears 15 bulbs, *Liriomyza ornata* (Meig.) — over 40, like *L. virgo* (Zett.). In *Campanulomyza* gen. nov. the number of bulbs varies from 3 to 5 (cf. de Meijere, 1937). In the natural genus *Calycomyza* Hend. the more plesiomorphous *C. artemisiae* (Kalt.) bears three bulbs, while

the apomorphous species — about 10. In the natural genus *Cerodontha* Rond. spiracles bearing three crevices on finger-like bulbs characterize the subgenera: *Dizygomyza* Hend. s. str. and *Pooemyza* Hend., while in *Cerodontha* Rond. s. str. and *C. flavocingulata* (Strobl) the number of pores exceeds 15. *Irenomyia* Nowak. bears three bulbs [Fig. 40], *Haplomyza* Hend. — 6 bulbs, *Xeniomyza* Her. in Meij. — 8 bulbs.

The number of bulbs in *Phytomyza* Fall. s. l. is not less than 7 but it may exceed even 100. Within the numerous natural genera, into which the group should be divided, spiracles show parallel differentiation series which resemble orthogenetic series or allometric growth series and clearly demonstrate the deviation rule [Fig. 41—52]. Certain variability ranges of number of bulbs e. g. 7—10, 10—15, 14—20, 20—28, occur repeatedly. These ranges are broad enough within the particular species. They may overlap or even be identical not only in species belonging to different natural groups but also in species closely related, e. g. in *Phytomyza obscura* Hend. and *Ph. origani* Her., in *Ph. tanaceti* Hend. and *Ph. klimeschi* Her., in *Ph. angelicae* Kalt. and *Ph. selini* Her. It may be assumed that the lack of divergency of the plastic larval features is often due to the so-called convergence (more strictly parallelism) of races (Hennig, 1950), which is to be expected especially in conditions of a directional and parallel evolution. In descendent species originating from a common ancestor there may occur independently a similar apomorphous feature, e. g. increase of the number of bulbs up to the same average level.

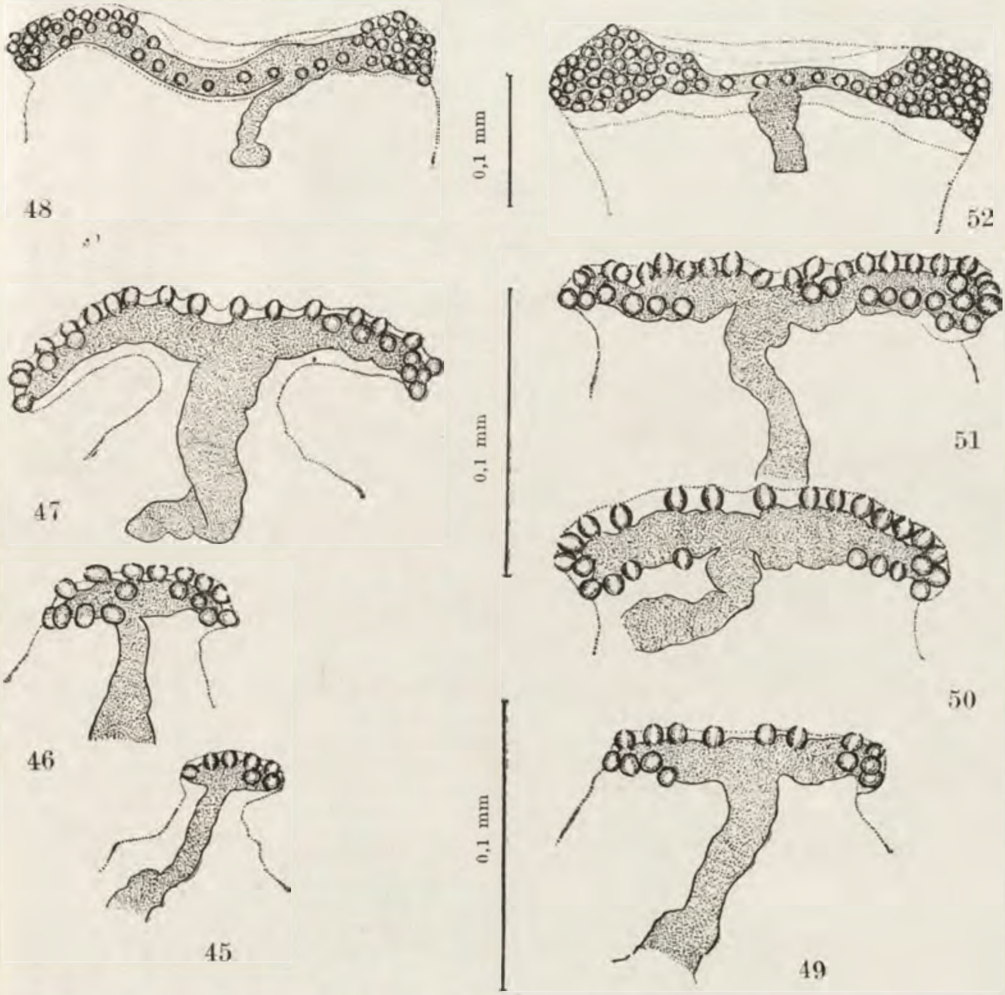
The evolutionary process consisting in the growth of the number of spiracular bulbs bearing respirative pores is an example of polymerization of homotypic parts. Some remarkable acceleration of the process [cf. e. g. fig. 43—44] may be interpreted by assuming that in ontogenetic and phylogenetic developments the number of bulbs increases not only by addition (i. e. division of only certain embryonal buds) but also by multiplication (i. e. more or less simultaneous division of all the buds). This is confirmed by cases of multiplication (mostly duplication) of the number of bulbs in closely related species [Fig. 53—58] as well as by those of a regular grouping of bulbs. Primary bulbs (primäre Knospen) bear at times several secondary bulbs (sekundäre Knospen). It is strikingly remarkable in the Javanese *Agromyza tephrosiae* Meij. (three triple bulbs), in *Liriomyza ornata* (Meig.) (12 bulbs — double to fourfold, de Meijere, 1938) and in the Japanese *Phytomyza kisakai* Sasak. (39—44 bulbs in 10 groups, Sasakawa, 1954b). Variability of the number of secondary bulbs indicates some combination of multiplication with addition.

Polymerization of the bulbs is accompanied by general growth of the spiracle, which is, at the same time, an allometric growth. The remarkable acceleration and correlation of both processes must be noticed. A hypertrophy of the organ seems to result from the critical point of the allometric growth being surpassed. It may be observed particularly in *Phytomyza calthivora* Hend. (cf. fig. 44 and p. 131).



41

Fig. 41—52. Parallel differentiation series of posterior larval spiracles in *Phytomyza* FALL. s. str.: 41—44 — the group of *Ph. abdominalis* ZETT. (on *Ranunculaceae*): 41 — *Ph. campanariae* NOWAK. [from *Pulsatilla pratensis* (L.) MILL., Kampinos Forest, Granica, 31 VII 1955, leg. J. T. NOWAKOWSKI], 42 — *Ph. albimargo* HER. (from *Anemone nemorosa* L., Parkowo near Poznań, 26 V 1951, leg. J. T. NOWAKOWSKI), 43 — *Ph. calthophila* HER. (from *Caltha palustris* L., Granica, 7 VII 1955, leg. J. T. NOWAKOWSKI), 44 — *Ph. calthivora* HEND. (from *Caltha palustris* L., Młociny near Warszawa, 3 VII 1957, leg. J. T. NOWAKOWSKI); 45—48: the group of *Ph. rectae* HEND., (on *Ranunculaceae*): 45 — *Ph. rectae pulsatillae* HER. [from *Pulsatilla pratensis* (L.) MILL., Kampinos Forest, Łuże, 26 IX 1954, leg. J. T. NOWAKOWSKI], 46 — *Ph. hendeli* HER. (from *Anemone ne-*



morosa L., Reservation Granica, 8 VII 1955, leg. J. T. Nowakowski), 47 — *Ph. ranunculivora* Her. (from *Ranunculus repens* L., Młociny, 21 X 1955, leg. J. T. Nowakowski), 48 — *Ph. linguae* Lundq. (from *Ranunculus flammula* L., Reservation Sieraków, 13 IX 1955, leg. J. T. Nowakowski); 49—52: the group of *Ph. spondylii* R. D. (on *Umbelliferae*): 49 — *Ph. spondylii* R. D. (from *Heracleum sphondylium* L., Tatry, Dolina Bystrej, 20 IX 1953, leg. J. T. Nowakowski), 50 — *Ph. pastinacae* Hend. (from *Pastinaca sativa* L., Łagów, 10 VI 1950, leg. J. T. Nowakowski), 51 — *Ph. sii* Her. (from *Sium latifolium* L., Kampinos-Forest, Sadowa, 27 VII 1957, leg. J. T. Nowakowski), 52 — *Ph. cicutae* Hend. (from *Cicuta virosa* L., Polish Pomerania, Słupsk, 6 VIII 1925, leg. O. Karl).

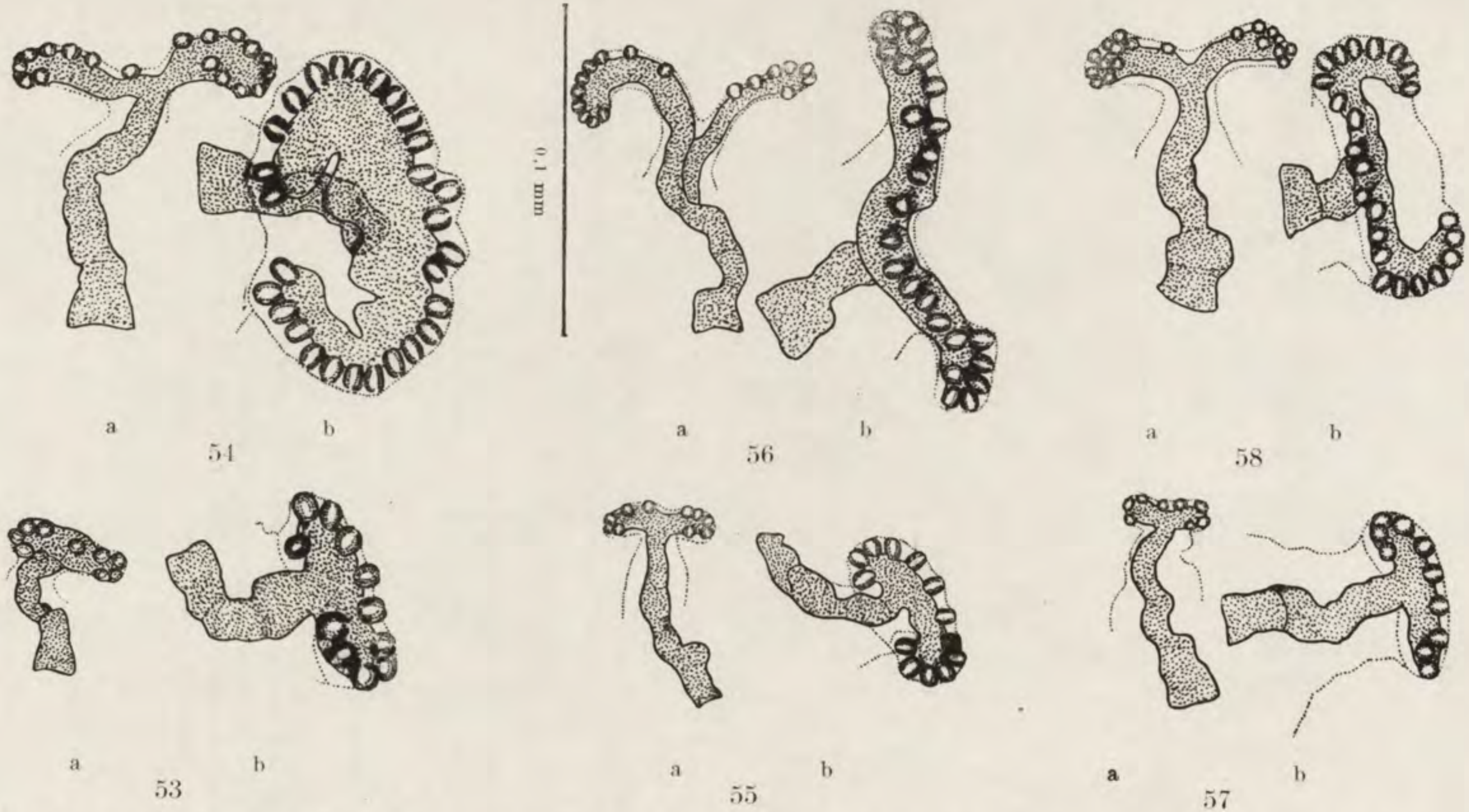


Fig. 53—58. Parallel duplication of the average number of bulbs in the anterior (a) and posterior (b) larval spiracles in some groups of *Phytomyza* Fall., s. str.: 53 — *Ph. obscura* Hend. [from *Satureja vulgaris* (L.) Fritsch., Kampinos-Forest, Reservation Sieraków, 19 IX 1954], 54 — *Ph. tetrasticha* Hend. (from *Mentha aquatica* L., Promno near Poznań, 13 X 1951), 55 — *Ph. nepetae* Hend. (from *Nepeta cataria* L., Kiekrz at Poznań, 17 VII 1951), 56 — *Ph. lycopi* Nowak. (from *Lycopus europaeus* L., Reservation Sieraków, 22 IX 1955), 57 — *Ph. lithospermi* Nowak., (from *Lithospermum officinale* L., Łomianki near Warszawa, 22 VI 1957), 58 — *Ph. symphyti* Hend. (from *Symphytum officinale* L., Rokietnica near Poznań, 24 VI 1951). After Nowakowski, 1959, modified.

Evolution gives rise to several types of spiracles. The increase in the number of bulbs is associated with an enlargement of the atrium which ramifies usually into two branches with slightly bent ends. If the branches of the atrium are very short or markedly bent then an "oval" type of the spiracle results: the top shield of the spiracular process is round, oval or kidney-shaped, with bulbs arranged in the shape of a crown, a horse-shoe or an open ellipse [Fig. 41, 42, 45, 53b, 54b, 55b, 57b]. Occasionally the edge of the ellipse is deeply indented and thus the atrium appears to be star-shaped, e. g. in *Phytomyza asteris* HEND., *Ph. adenostylis* HER. If the branches of the atrium markedly extend being bent only slightly, the top shield of the spiracle develops into two "horns" and the "two-horned" type of spiracle results. According to the length of the horns two types are distinguished: a "short two-horned" (kurz zweihörnig) type often found especially in the anterior spiracles [Fig. 53a, 55a, 57a] and a "long two-horned" (lang zweihörnig) one [Fig. 47, 56b]. Some cases show enormous lengthening of the horns, with coresponding directional widening of the spiracular process, the whole organ adopting the shape of a ledge protruding out of the puparium [Fig. 43, 44, 48, 51, 52]. Horns are never of the same length. In case when one of them is very slightly developed and the other markedly extended, then there occurs the "single-horned" (einhörnig) type of spiracle, e. g. in *Napomyza glechomae* (KALT.), *Phytomyza milii* KALT., *Ph. fallaciosa* BRI. [Fig. 26]. More rarely a marked increase in the number of bulbs is accompanied by tree-like ramification of the atrium and the spiracle may become of an antler-like shape as well. This form of spiracle is found in species feeding in stem pith, e. g. in *Ophiomyia ranunculicaulis* HER. (on *Ranunculus* L.) and *Phytomyza flavicornis* FALL. (on *Urtica* L.).

The directional evolution of the spiracles in endophagous larvae has clearly adaptive character, giving an example of caenogenesis (sensu SEWERTZOFF, 1931). An enlargement of the spiracle through its growth and ramification together with a simultaneous increase in the number of respiratory pores able to close is an adaptation to living in a moist environment in which it is difficult to respire. This adaptation could render the gaseous diffusion between the tracheae and the environment more efficient and protect the spiracle against being completely plunged in liquid constituents of the larval frass, in cell sap flowing out of torn plant tissue or in rain water often entering inside the mine.

HENNIG (1950) finds the number of spiracular pores in cyclorrhaphous larvae to be remarkably greater in saprophagous forms than in free living or feeding in live plant tissues. This would seem to be contradicted by the enormous increase in the number of bulbs in phytophagous larvae of the *Agromyzidae*, which originated — may be indirectly — from saprophagous forms. Respiratory conditions in the green living parts of plants are, in fact, more advantageous than in dead and decaying parts. However, even inside the mine there must be an oxygen deficiency at night time when the plant ceases to give it off. Besides, the polymerization of bulbs advances farthest in larvae feeding in

greenless stem pith (see above) or in those mining in leaves or stems of marshy plants exposed to submergence[1].

In miners of leaves and stems of marshy plants (helophytes) an increase in the number of spiracular bulbs is associated with an adaptation of the spiracular processes to an additional clinging function [Fig. 59—65]. As marshy or watery ground where helophytes grow does not favour the pupation of larvae or, even more so, the emergence of adults from puparia, the larvae

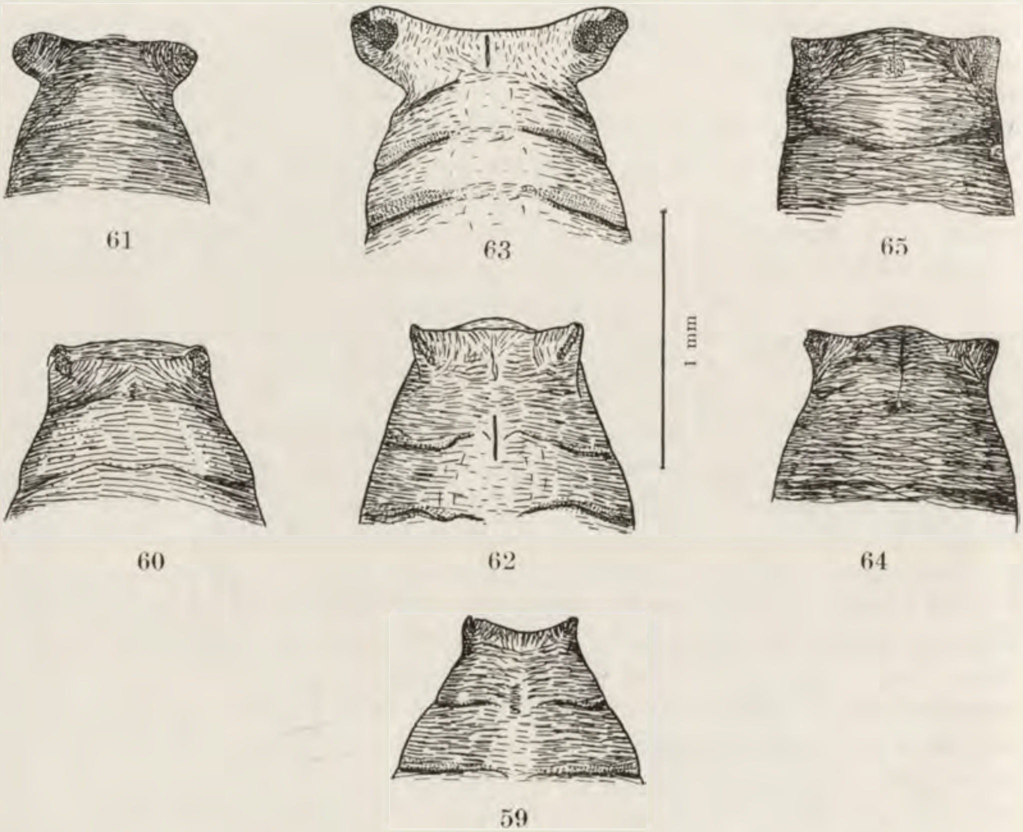


Fig. 59—65. Parallel adaptation of the posterior larval spiracles to the clinging function in species mining in masrsh plants. Terminal part of puparium of: 59 — *Phytomyza angelicastri* Her. (from *Angelica silvestris* L.), 60 — *Phytomyza linguae* Lundq. (from *Ranunculus flammula* L.), 61 — *Liriomyza virgo* (Zett.) (from *Equisetum limosum* L.), 62 — *Phytomyza sii* Her. (from *Sium latifolium* L.), 63 — *Phytomyza cicutae* Hend. (from *Cicuta virosa* L.), 64 — *Phytomyza calthophila* Her. (from *Caltha palustris* L.), 65 — *Phytomyza calthivora* Hend. (from *Caltha palustris* L.).

[1] Exceptions are in this respect: *Agromyza lathyri* Hend. (on *Lathyrus* L.) and *Japanagromyza quercus* Sasak. (on *Quercus* L.) bearing over 40 bulbs.

pupate on the leaves or stems of the host plants, clinging with their posterior spiracles to the exit slit of the mine. As a result their posterior spiracular processes are strongly developed and diverge laterally, thus resembling a crutch. Such a clinging organ securing puparia against plunging into water was observed by Hering (1951a) in three species belonging to two different genera, i. e. in *Liriomyza virgo* (Zett.) (on *Equisetum limosum* L. and *E. palustre* L., fig. 61), in *Phytomyza cicutae* Hend. (on *Cicuta virosa* L., fig. 63) and *Phytomyza calthivora* Hend. (on *Caltha palustris* L., fig. 65). The author has found similar though less developed adaptations in three more species, i. e. in *Phytomyza sii* Her. (on *Sium latifolium* L. and *Berula angustifolia* L., fig. 62), in *Ph. calthophila* Her. (on *Caltha palustris* L. and *C. laeta* Sch. N. K., fig. 64) and in *Ph. linguae* Lundq. (on *Ranunculus lingua* L. and *R. flammula* L., fig. 60). Among these six similar forms there are two pairs of closely related species: *Phytomyza sii* Her. with *Ph. cicutae* Hend. and especially *Ph. calthophila* Her. with *Ph. calthivora* Hend. In each of the two pairs the latter species shows not only a better developed clinging organ (i. e. a more than twice as long spiracular process as in the former species) but it has also 2—3 times larger number of bulbs, if compared with the former species, thus representing a higher level in a series of growing apomorphy [Fig. 43—44, 51—52]. There is every reason to believe that the pair of miners of *Caltha* L. — *Phytomyza calthophila* Her. and *Ph. calthivora* Hend. — originated from an direct common ancestor, the former of the quoted descendents only slightly deviating from this ancestor so that it represents approximately the starting level of the latter descendent.

Spiracles being well adapted to the clinging function bear here, at the same time, the largest numbers of bulbs, and they occupy the highest level within the series of growing apomorphy, thus being the end result of an evolutionary trend. Some tendency to develop such clinging organs may be observed in certain other species, first of all in representatives of *Phytomyza* Fall. s. l. mining in marsh plants, e. g. in *Napomyza buhriana* Her. (on *Ranunculus sceleratus* L. and *R. repens* L.), *Phytomyza archangelicae* (on *Archangelica litoralis* Fr.), *Ph. calthae* Her. (on *Caltha palustris* L.), *Ph. phellandrii* Her. [on *Cicuta virosa* L. and *Oenanthe aquatica* (L.) Poir.], moreover in *Liriomyza ornata* (Meig.) (on *Butomus umbellatus* L.). This tendency can also be seen in certain species which are only partially connected with marsh plants or marshy habitats, e. g. in *Phytomyza angelicastri* Her. (on *Angelica silvestris* L., fig. 59), *Ph. ranunculi* (Schrk.) and *Ph. ranunculivora* Her. (on *Ranunculus acer* L., *R. repens* L., *R. lanuginosus* L. etc.), the latter species representing the starting level for *Ph. linguae* Lundq. [Fig. 47—48] to which it is closely related. A morphological tendency to develop the clinging organ is always accompanied by the habit of sticking to the exit slit of the mine. A puparium with its "crutch" not adequately developed sticks but slightly to the leaf, tears off readily and falls into the water or to the muddy ground.

In such conditions it may be seen how an adaptative character maintains itself and develops by the operation of natural selection.

An adaptative trend may be explained by orthoselection, i. e. by uni-directional selection pressure in constant environmental conditions. Orthoselection arranges random mutations into one successive series. Besides, there is not to be excluded a tendency to directional mutations (a mutational pressure) resulting from long-lasting orthoselection or even due to a direct environmental influence, the more so as mutagenic factors are more broadly comprehended now. The material for parallel evolution form parallel mutations (Vavilov's law of homologous series) systematized by orthoselection into successive series (cf. Huxley, 1942; Simpson, 1944; Hennig, 1950; Remane, 1952).

It is well known that especially parasitic groups evolve in a directional and parallel way, for related parasites react in a similar manner to influences exerted by similar host organisms (cf. Szidat, 1956). The parasitic life of the *Agromyzidae* is a direct cause of caenogenetic trends, that is of evolutionary trends of the larvae: the diminishing of the body size and the enlargement of spiracles associated with polymerization of their openings. Nevertheless, the decrease in the larval body size brings about a decrease in the adult body size, this tendency seems to be followed by the other two trends found merely in the evolution of the adults, i. e. by the oligomerization of bristles and by the reduction of wing venation, the latter being caused by the costalization as well. Costalization could depend on flight mechanics which, in turn, influences a decrease of the adult body size and then a reduction of wing venation and of bristles too.

The subtle difference between divergent speciation and evolution in its stricter sense (something like phyletic evolution; Simpson, 1944) is far easier to grasp in conditions of directional and parallel development of a group. A species may evolve in certain characters and still remain a single interbreeding community. E. g. individuals of *Agromyza intermittens* Beck. that had completely lost t_p [Fig. 29], these which show partial reduction of the vein, as well as those which have it wholly preserved belong to the same interbreeding community. Even in the case of an atrophy of t_p in all the individuals, which may appear in the future, they will still constitute the same species — *Agromyza intermittens* Beck., and not a new successive descendent species, if this morphological change is not connected with a change of the ecological niche and a sexual alienation of the altered individuals. Similarly, the proximal shifting of t_p does not mean a transformation of *Cerodontha flavocingulata* (Strobl) into "*Phytagromyza spinicauda* Hend." (cf. p. 119); the discrimination of the latter in an example of a horizontal division made in this case even intraspecifically. On the other hand, a splitting of an interbreeding community, as effected by adaptation to various host plants and by differentiation of the genital apparatus, may proceed without advance in certain processes of direct-

ional evolution. In this way the genital apparatus as well as ecological niche characters are of more important taxonomic value than external features of adults or larval features evolving directionally. It is just one of the main tasks of taxonomy to distinguish between characters resulting from divergent speciation and those due to the directional evolution within a group.

REMARKS ON HOST PLANT SELECTION BY MINING FLIES

Host Plant Specificity

The specificity of host-parasite relation in the *Agromyzidae* has already been stressed. The larvae of a given Agromyzid species feed only on certain definite plant species (host specificity), in a certain plant organ and tissue (topospecificity) and in a certain definite way. These strictly defined food and living requirements and feeding habits of the larvae constitute important taxonomic features, and they make it possible to use the host-parasite discrimination method.

The host plant specificity of phytophagous insects, being mainly the result of their food specialization is, after all, narrower in general, than it might have seemed upon superficial observations. It is monophagy and restricted oligophagy that prevails in most groups (Brues, 1946). The picture has often been confused by erroneous data in the literature, however, a more careful study of a given group of phytophagous insects in nature, shows as a rule certain more definite food requirements (cf. Heikertinger, 1951).

Similarly, as studies on mining insects advance, alleged polyphagous species have often proved to be, in fact, limited oligophagous or even monophagous. To realize better how much progress has been made in this field it is hardly necessary to resort to XIX-century works, it is sufficient to compare the latest valuable work of Hering (1957a) with certain papers of the twenties or even thirties of this century. However, even this recent work requires further corrections in this respect. For example it could be recalled how the list of host plants of *Phytomyza obscura* Hend. changed within the last 40 years:

Hendel, 1920 — *Labiatae*: *Satureja* L. s. l., *Galeopsis* L.; *Compositae*: *Arctium* L.
Hering, 1927 — *Labiatae*: *Satureja* L. s. l., *Origanum* L.; *Boraginaceae*: *Symphytum* L.
Hendel, 1936 — *Labiatae*: *Satureja* L. s. l., *Origanum* L., *Mentha* L., *Lycopus* L., *Galeopsis* L., *Nepeta* L.
Hering, 1935—1937, 1957 — *Labiatae*: *Satureja* L. s. l., *Origanum* L. (*Ph. o. origani* Her.), *Mentha* L. (*Ph. obscura* Hend. and *Ph. o. tetrasticha* Hend.), *Lycopus* L., *Galeopsis* L., *Nepeta* L. and *Dracocephalum* L. (*Ph. o. nepetae* Hend.).
Nowakowski, 1959 — *Labiatae*: *Satureja* L. s. l.

These misidentifications have resulted from the similarity of *Phytomyza obscura* Hend. in mine, larva or external adult morphology to

- *Phytomyza lappivora* Hend.? (on *Arctium* L.)
- *Phytomyza symphyti* Hend. (on *Symphytum* L.)
- *Liriomyza eupatorii* (Kalt.) (on *Galeopsis* L.)
- *Phytomyza nepetae* Hend. (on *Nepeta* L.)
- *Phytomyza lycopi* Nowak. (on *Lycopus* L.)
- *Phytomyza tetrasticha* Hend. (on *Mentha* L.)
- *Phytomyza origani* Her. (on *Origanum* L.).

Strict monophagy, on the other hand, corresponding to strict host plant specificity is rather rare if it does not result from the plant genus being monotypic (cf. Tempere, 1946; Heikertinger, 1931). Many a time an insect species is considered to be strictly monophagous for the simple reason that its host plant genus is represented by a single autochtonic species in a given area, and yet the insect in question behaves as an oligophagous one as regards allochthonic plant species or else when found in some other areas. While investigating mining insects in botanical gardens, Buhr (1932, 1937, 1941, 1954) discovered many such cases. The same phytophagous fauna feeds on closely related and slightly differentiated plant species, hybridizing ones in particular. That is why Voigt (1932) and Hering (1926, 1951a) were correct in extending the notion of monophagy to include certain kinds of restricted oligophagy, occuring most frequently among phytophagous insects. Besides monophagy of the first degree (strict monophagy) Hering (1951a) distinguished monophagy of the second degree (a particular phytophagous species feeding on a single plant section or subgenus) and monophagy of the third degree (a particular phytophagous species feeding on a single plant genus). Voigt (1932) having restricted the notion of oligophagy, distinguished systematic oligophagy (a particular phytophagous species feeding on related plants) and disjunctive oligophagy (a particular phytophagous species feeding on a relatively small number of unrelated plants). These two kinds of oligophagy form together the combined oligophagy (Heikertinger, cf. Hering, 1951a). Hering (1951a) defined three degrees of systematic oligophagy: the first degree means a phytophagous species feeding on representatives of various plant genera belonging to the same family, the second — that on representatives of various plant families of the same order, the third — that on those of a number of different but related plant orders. This classification cannot be, of course, nothing but a relative one.

Among the *Agromyzidae* monophagy of the second and that of the third degree are most common, systematic oligophagy of the first degree being frequent too: within the latter, however, a number of subdegrees of an ever lower frequency should be distinguished, namely a phytophagous species feeding on a number of closely related plant genera (e. g. *Napomyza aconitophila* Hend., *Phytomyza aconiti* Hend. or *Ph. aconitella* Hend. on *Aconitum* L. and *Delphinium* L.), on a plant tribe [e. g. *Phytomyza affinis* Fall. on

Cynareae (except *Arctium* L.) or *Ph. conyzae* HEND. on *Inuleae*], on a plant subfamily (e. g. *Agromyza spiraeae* KALT. on *Rosoideae* or *Phytomyza sonchi* R. D. on *Liguliflorae*), and finally on nearly a whole family [e. g. *Trilobomyza labiatarum* (HEND.) on *Labiatae*].

Before we proceed to discuss the oligophagy of higher degrees and polyphagy, the species of more concealed larval life habits, i. e. those feeding in cambium, in stem pith, stem basis, roots or on the hypanthium, in fruit or seeds, must be dealt with separately. The feeding requirements of these species have not been fully discovered so far, yet as it results from certain more recent investigations, monophagy seems to prevail here too. KANGAS (1937) has assumed that every single species of *Dendromyza* HEND. is linked with a single tree genus. HERING (1957b) and SPENCER (1957c) have shown a more narrow host specificity of certain representatives of *Melanagromyza* HEND., feeding in stem pith. *Melanagromyza aeneiventris* (FALL.) and *M. lappae* (LOEW), very similar to each other and both feeding in stems of *Compositae* and *Umbelliferae* (the former species also in those of *Urtica* L.), have proved to be complexes of monophagous species differentiated mainly in the larval stage. A number of monophagous species of *Ophiomyia* BRASCHN. was discovered earlier; they live in stems but often resemble *O. maura* (MEIG.) producing a very long linear mine in the leaves of *Solidago* L., *Aster* L. and *Erigeron* L. (*Compositae*). The information given by ALLEN (1956) that this species had been found in the stem of *Heracleum* L. (*Umbelliferae*) too, was next corrected by SPENCER (1957b) and by ALLEN herself (1958). As far as the present data are concerned, *Napomyza lateralis* (FALL.) is the only polyphagous species among non-leaf miners; it occurs on *Compositae* and *Umbelliferae* and also on *Campanulaceae*, *Verbenaceae*, *Scrophulariaceae*, *Ranunculaceae* and *Urticaceae* (HENDEL, 1934). A certain lack of host specificity is accompanied here by a lack of topospecificity of the parasite that may live in inflorescences, stems, stem bases and leaf petioles, giving rise to some deformations of these plant organs (BUHR, 1955). But this very variable parasite may also constitute a group of sibling species, each of more restricted feeding habits.

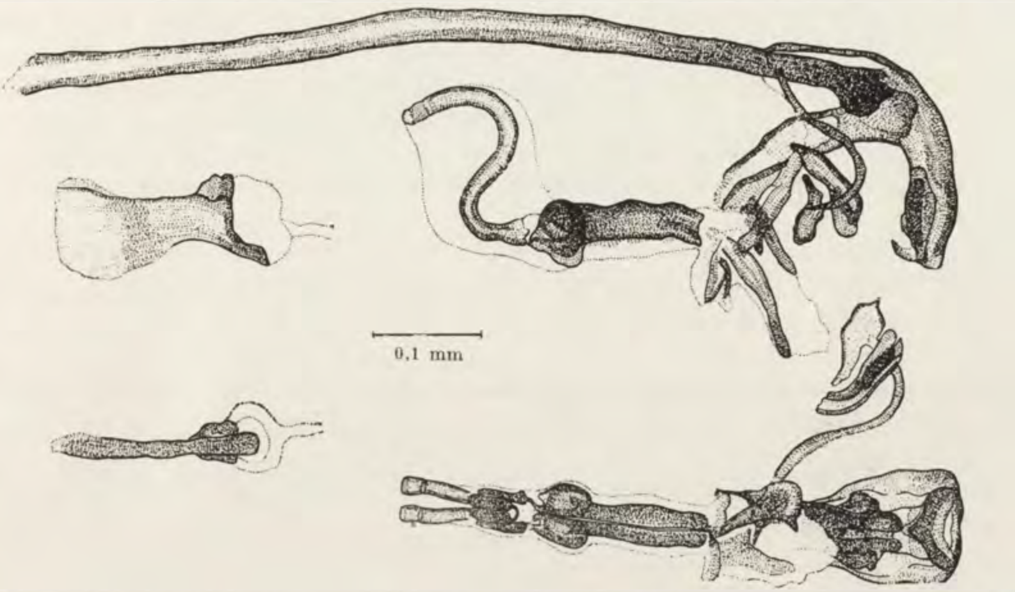
As regards leaf mining *Agromyzidae* one case of systematic oligophagy of the second degree is known to occur: *Trilobomyza flavifrons* (MEIG.), a common parasite of the *Caryophyllaceae*, occurs at times also on *Beta* L. and *Chenopodium* L. (HERING, 1951a, 1957a) belonging to the closely related family *Chenopodiaceae* (order *Centrospermae*).

Cerodontha (*Dizygomyza*) *luctuosa* (MEIG.) that was supposed to feed on *Carex* L. and exceptionally on *Eriophorum* L. (*Cyperaceae*, *Cyperales*), and besides on members of the group of *Juncus effusus* L. (*Juncaceae*, *Liliiflorae*) was thus regarded as showing systematic oligophagy of the third degree (HENDEL, 1931; HERING, 1937, 1951a, 1957a). Though the form living on *Juncus effusus* L. has already been distinguished by KARL (1926) as *Dizygomyza effusi* KARL, it was not, however, characterized by any essential morphological

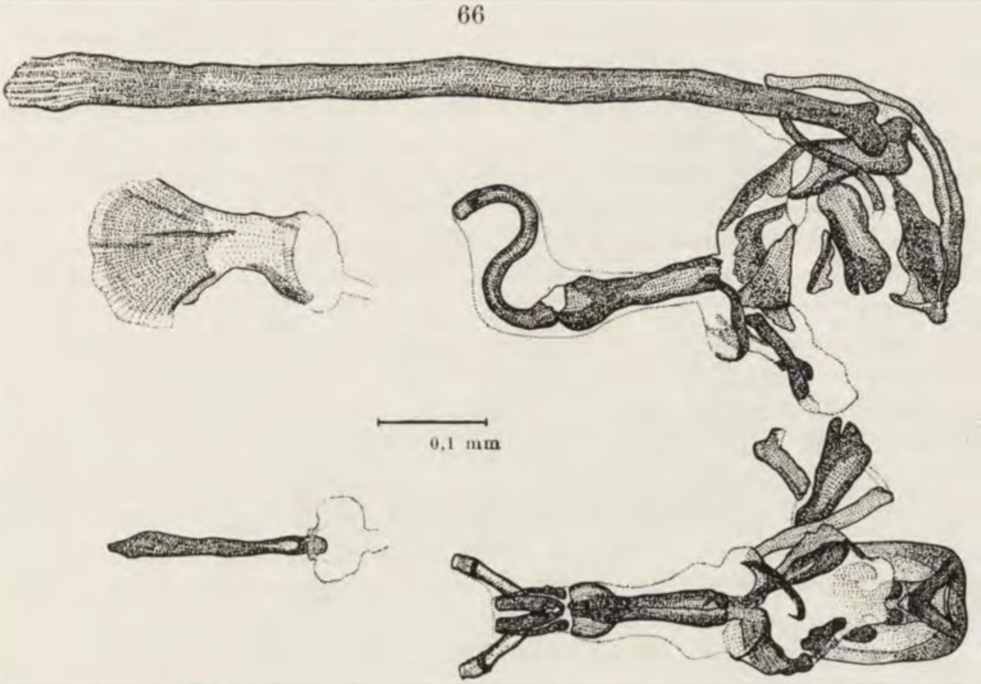
features. Neither could de Meijere (1928, 1941) distinguish *D. effusi* Karl on the basis of larval characters. Groschke (1955) recognized the species by finding some differences in the mine and alleged differences in the coloration of the puparia. Hering (1957a) treated it lately as a subspecies. It was not until the author had examined the genitalia of the males reared from *Carex hirta* L. (2 ♂♂ emerged on 14 V 1956, mines found on 3 XI 1955 at Cybulice in the Kampinos-Forest, 1 ♂ emerged on 24 VII 1925, mines found by E. M. Hering at Berlin-Frohnau) and from *Juncus effusus* L. (1 ♂ emerged on 21 I 1926, mines found by O. Karl at Słuspk in the Polish Pomerania, 2 ♂♂ emerged on 11 V 1956, mines found on 17 X 1955 in the Reservation Granica in the Kampinos-Forest, 1 ♂ emerged on 4 VI 1958, mines found on 7 XI 1957 in the same Reservation) that the specific distinctness of *Cerodontha* (*Dizygomyza*) *effusi* (Karl) was proved definitely [cf. fig. 66—67].

Trilobomyza verbasci (Bché), more closely connected with *Scrophularia* L. and *Verbascum* L. (*Scrophulariaceae*, *Tubiflorae*), was recently found repeatedly on *Buddleia variabilis* Hemsl. (cf. Hering, 1951a; Buhr, 1954) which was till now included in the *Loganiaceae* (order *Contortae*). This phenomenon was interpreted as xenophagy bordering on systematic oligophagy of the third degree (cf. Hering, 1951a). However, by courtesy of Professor Hering (in litt.) we learn that in the modern system of plants *Buddleia* L. will be included in the *Scrophulariaceae*, thus *Trilobomyza verbasci* (Bché) showing systematic oligophagy of the first degree.

In the *Agromyzidae* there is no proper disjunctive oligophagy, however, three cases of combined oligophagy are known to occur here. *Agromyza reptans* Fall., a common miner of *Urtica* L., feeds on other *Urticaceae* too: on *Parietaria* L. and *Laportea* L., as well as on *Cannabaceae*: on *Cannabis sativa* L., *C. gigantea* hort. and *Humulus japonica* Sieb. et Zucc. (Buhr, 1937, 1954), thus being attached to the order *Urticales* and showing systematic oligophagy of the second degree. But observations made by Buhr (1937) in the Botanical Garden at Rostock showed that larvae of this species were feeding and attained their full development also on *Mentzelia albicaulis* Dougl. and *M. lindleyi* Torr. et Gray (*Loasaceae*, *Parietales*). *Liriomyza brassicae* (Rill.) (= *L. cruciferarum* Her.) closely linked with the *Cruciferae* feeds not only on the *Resedaceae* and the *Capparidaceae*, also belonging to the order *Rhoeadales*, but also on *Tropaeolum* L., a representative of the order *Gruinales* (Buhr, 1937). The two mentioned cases of combined oligophagy may be explained by biochemical similarity of these unrelated host plant groups (cf. p. 143). Only a single exceptional case of an oligophagous species feeding on unrelated plants, between which no phytochemical affinity has been shown till now, is still to be explained: *Liriomyza eupatorii* (Kalt.) makes a serpentine mine (heliconome) on *Galeopsis* L. (*Labiatae*) as well as on *Eupatorium* L. and more rarely on other *Compositae*, such as *Solidago* L., *Aster* L., *Helianthus* L. and *Lapsana* L. (Hering, 1957a). Originally, a form mining similarly on *Cannabis*



66



67

Fig. 66—67. A pair of monophagous sibling species, treated till now as a single oligophagous species. Male copulatory apparatus of: 66 — *Cerodontha* (*Dizygomyza*) *luctuosa* (Meig.) (from *Carex hirta* L., Berlin-Frohnau, 24 VII 1925, leg. M. Hering), 67 — *Cerodontha* (*Dizygomyza*) *effusi* (Karl) (from *Juncus effusus* L., Kampinos Forest, Reservation Sieraków, 11 V 1956, leg. J. T. Nowakowski).

L. (*Cannabaceae*) was included in this species. Due to certain slight colour differences, HENDEL (1931) had distinguished this form as *Liriomyza cannabis* HEND. BUHR (1937), however, succeded in his experimental transplantation of the larvae from *Cannabis* L. to *Eupatorium* L. and back from *Eupatorium* L. to *Cannabis* L., and also from *Cannabis* L. to *Galeopsis* L., without stopping the developmental cycle of the insect. While examining the genital apparatus, the author has found no differences between males reared from *Eupatorium cannabinum* L. and from *Galeopsis pubescens* BESS., and nothing but slight peculiarities regarding males reared from *Cannabis sativa* L. have been noticed. Thus, if the forms feeding on the plants mentioned are two or even three sibling species by now, they all must have quite recently been but one species attached to representatives of three completely unrelated plant families.

We know but four polyphagous species of leaf mining *Agromyzidae*: *Phytomyza atricornis* MEIG., *Liriomyza strigata* (MEIG.), *L. bryoniae* (KALT.) and *L.* (*Cephalomyza*) *cruciferricola* (HER.). It is uncertain whether their polyphagy is still fully maintained at present but there is no doubt that it is a secondary one. The four species mentioned have certain host requirements too, since though they occur on numerous and frequently unrelated plants, they still keep avoiding certain plant groups and species, they also reveal obvious preferences for certain taxonomic and ecological groups of their host plants (cf. pp. 155–156). Polyphagy of a species is not always accompanied by its common occurrence and at any rate by its uniform distribution on the flora and vegetation (cf. pp. 144, 155–156).

The occurrence of a phytophagous species on its specific host plants, termed by VOIGT (1932) primary substrata (primäre Substrate), is referred to by him as euphagy (Euphagie). Xenophagy (Xenophagie) is the reverse of that notion. That is an exceptional occurrence of a phytophagous species on a non-specific host plant termed secondary substratum (sekundäres Substrat). Xenophagy in its strict sense applies merely to cases in which a non-specific host plant is neither related to the specific one nor similar to it phytochemically. VOIGT (1932), HERING (1951a, 1957a) and certain other authors gave a number of examples of such "errors" committed by mining insects in their choice of host plants. HERING (1951a) even put forward a supposition that cases of erroneous oviposition on non-specific host plants were quite common in nature and yet escaped our attention. The reason is that larvae having unsuitable food die before they attain their full development.

However, not a single case of xenophagy (in the strict sense) was found in the large number of leaf mines we had collected and examined. We believe therefore that the phenomenon concerned occurs extremely seldom and is quite exceptional in the *Agromyzidae*. The examples given in the literature, do not seem trustworthy as a rule. We are just bound to suspect that they have resulted from misidentification of plants or from that of new insect species. Thus for instance, the information that *Trilobomyza flavifrons* (MEIG.) had been

found on *Stachys germanica* L. (*Labiatae*) was lately corrected by HERING himself (1957a) as probably resulting from *Lychnis coronaria* DESV. (*Caryophyllaceae*) being taken for the former plant concerned. Some *Caryophyllaceae* were mistaken for other plants or some mines were misidentified, thus explaining three further cases of "xenophagy" of *Trilobomyza flavifrons* (MEIG.): on *Lysimachia nemorum* L. (*Primulaceae*, STARÝ, 1930), on *Anthyllis vulneraria* L. (*Leguminosae*, RYDÉN, 1955) and on *Galinsoga* RUIZ. et PAV. (*Compositae*, HERING, 1957a). The information that *Cerodontha* (*Dizygomyza*) *iraeos* (GOUR.) had been found on *Typha latifolia* L. (*Typhaceae*) was due to a misidentification of *Iris pseudacorus* L. (*Iridaceae*; cf. HENDEL, 1931; HERING, 1957a). BRISCHKE's (1881) information on *Liriomyza impatientis* (BRI.) as being found on *Circaea lutetiana* L. (*Oenotheraceae*) was probably due to his taking *Impatiens nolitangere* L. (*Balsaminaceae*) for the former plant. In KARL's collection the author has found a male specimen of *Napomyza glechomae* (KALT.), labelled as having been reared (13 II 1925) from *Veronica chamaedrys* L. (*Scrophulariaceae*, the mine collected near Słupsk in Polish Pomerania). The plant in question, however, grows so frequently together with *Glechoma hederacea* L. (*Labiatae*) and the lower leaves of both plants are at times so similar that they could be mistaken for each other. HERING (1936) reported finding of "*Phytagromyza similis* (BRI.)" a miner of *Knautia* L. (*Dipsacaceae*), on *Centaurea atropurpurea* WEDDST. et KIT. (*Compositae*), but subsequently (1937) he described the reared specimens as a new species — "*Phytagromyza centaureana* HER." DE MEIJERE (1926) was said to have found larvae of *Phytomyza lappina* GOUR. on *Diervilla trifida* MNCH. (*Caprifoliaceae*) growing in the neighbourhood of *Arctium lappa* L. (*Compositae*) which was abundantly invaded by its parasite. But the uncertainty of this identification based exclusively on the larva and its mine can just be seen from the fact that two other species, namely *Phytomyza eupatorii* HEND. (on *Eupatorium cannabinum* L.) and *Ph. senecionis* KALT. (on *Senecio fuchsi* GMEL.) were simultaneously mistaken by DE MEIJERE for *Phytomyza lappina* GOUR. *Liriomyza trifolii* (BURG.) was found by BUHR (1953) on *Passiflora* spec. (*Passifloraceae*, *Parietales*) but as an empty mine only. Not a single case of xenophagy (in the strict sense) has been recorded by a specialist so far in an accurate and a more convincing manner, yet such cases could seem pretty common when identifying species on the ground of the external adult morphology. We do not deny that xenophagy exists as such, as the passing of phytophagous insects to non-specific plants. The example in the literature seem to show, however, that entomologists are more likely to be mistaken in identifying plants and insects than it is the case with insects in their choice of plants.

Cases bordering on xenophagy and systematic oligophagy, i. e. sporadic occurrence of a phytophagous species on plants closely related to its specific host plants, seem to be quite common among the *Agromyzidae*. The interpretation of many such a fact, however, is uncertain because of impossibility of

an exact species identification or of an inadequate knowledge of its ecology and geographic distribution. If no male has been reared from the larva found, it cannot at times be decided whether it was the presence of a known insect species on a non-specific host plant, i. e. xenophagy (in the broader sense), or the finding of a "new", i. e. so far unknown, insect species. For instance, the producer of leaf mine found by the author on *Prunus mahaleb* L. (in Poznań, 21 VI 1951) could have been either *Agromyza spiraeoidarum* Her., a miner of the *Spiraeoideae*, or *A. spiraeae* Kalt., a miner of the *Rosoideae*, or a "new" species closely related to them and linked with *Prunoideae* (cf. Hering, 1957a). Similarly, we can hardly be certain, whether *Phytomyza spondylii* R. D. closely connected with *Heracleum* L. has been a producer of certain linear mines found by Spencer on *Angelica* L. and *Astrantia* L. (cf. Hering, 1957a). At times, however, despite the exact identification of an insect species we cannot be certain, whether its "new" host plant has really been a non-specific one or whether it has been rather a specific but accessory (secondary) host plant. The classification of hosts as "primary (main)", "accessory (secondary)" or else "accidental, occasional (non-specific)" would be, of course, to a large extent an arbitrary one, since the parasite behaves towards them in a differently way depending on the ecological and geographic conditions and it is often differentiated into biological races, each connected with a particular host (cf. pp. 158—159). Whether a phytophagous species has passed to a non-specific host plant, may only be found when the plant is an allochthonic one originating from outside the distribution area of its parasite. Two species, for instance, living on *Erigeron acer* L.: *Phytomyza erigerophila* Her. and *Calycomyza humeralis* (Ros.) (the latter linked also with *Aster* L., *Bellis* L. and other allied plant genera, cf. Buhr, 1941) have moved to *Erigeron canadensis* L., a weed of North American origin, common in Europe. And yet *Erigeron canadensis* L. can be a secondary host for *Phytomyza erigerophila* Her. only, because *Calycomyza humeralis* (Ros.) occurs also in the Nearctic Region (Frick, 1952). Recently (on 25 VII 1956) the author has reared from this weed plant (growing at Łomianki near Warszawa) a male specimen of *Calycomyza solidaginis* (Kalt.), a miner of *Solidago virgaurea* L. and of *Erigeron acer* L. (cf. Hering, 1960), unknown in North America. Not all the cases of phytophagous insects moving to foreign plants grown in botanical gardens (cf. Buhr, 1932, 1937, 1941, 1954) could be assessed as, for the present, the distribution areas of most Agromyzid species remain unknown.

In the case where a phytophagous insect makes efforts to get a new host plant but cannot overcome its resistance, we speak of lethel oligophagy (Hering, 1951a). For instance, uncompleted mines with dead larvae of *Phytomyza heringiana* Hend., a parasite of *Malus silvestris* (L.) Mill., have been found on *Cydonia vulgaris* Pers. (Hering, 1957a), while dead larvae of *Liriomyza trifolii* (Burg.), a miner of a number of the native *Leguminosae*, — on *Robinia psudacacia* L. (Hering, 1952).

Influence of some Factors on Host Plant Choice

The plant choice made by a phytophagous insect and its ability to break direct plant resistance and resistance of its secondary environment, i. e. the pseudoresistance, depends on the whole of the specific and individual characters of both partners and on their physiological state at the given moment. This physiological state is determined, on the one hand, by the life rhytm of both partners and, on the other, by the secondary environment exerting an influence on the phytophagous insect both directly and indirectly, i. e. through its host plant. Among all the factors involved it is usually the one approaching the minimum that decides (cf. NUORTEVA, 1952). In approaching the subject from its ecological side, we shall try to grasp some factors of greatest importance, and to show by means of some concrete examples what influence they may exert.

It follows from the present discussion that among the *Agromyzidae* predominate kinds of host plant specificity that could be termed, as a whole, as systematic oligophagy (in the broadest sense), i. e. a phytophagous species feeding on a number of related species of host plants. Such dependence of host plant choice on their natural relationship, observed in most groups of phytophagous insects (cf. PETERSEN, 1930; BRUES, 1946; HEIKERTINGER, 1951; HERING, 1951a; NUORTEVA, 1952) is especially pronounced in the dipterous family discussed. However, considerable deviations from the prevailing principle exist here too. They are not merely cases of polyphagy and of combined oligophagy but also a lack of strict dependence of systematic oligophagy on the degree of the host plant relationship. An Agromyzid species may avoid certain plant species or genera within a larger systematic group of its hosts, or else it may occur eclusively on plant species or genera that are not considered as directly related. Thus, for instance, *Trilobomyza verbasci* (BCHÉ) feeds on *Scrophularia* L. and *Verbascum* L. belonging to two different subfamilies of the *Scrophulariaceae* but invades no representatives of other genera belonging to the above subfamilies. *Phytomyza pauliloewi* HEND., more closely connected with the group of *Peucedanum oreoselinum* (L.) MNCH., occurs also on *Pimpinella saxifraga* L. and *P. major* (L.) HUDS. but, on the other hand, avoids *Peucedanum palustre* (L.) MNCH. *Phytomyza rectae* HEND. s. l. occurs as biological subspecies (or perhaps sibling species) on *Clematis recta* L., *Atragene alpina* L. and *Pulsatilla* MILL., but occurs neither on *Clematis vitalba* L. nor on *Anemone* L. s. str. and *Hepatica* MILL. Further examples of similar deviations will be given when the influence of leaf structure as well as of the ecological character and geographic distribution of the plant on its choice by phytophagous insects will be discussed. Such slight breaks in host ranges can hardly by called disjunctive oligophagy, the more so in many a case they are controversial as the present plant system is still far from perfection

(cf. pp. 144—145). There is no doubt, however, that the influence exerted by many secondary factors modifies that of the main factor, namely that of the phylogenetic relationship of the host plants.

Oligophagy (in the broadest sense) is usually explained by phytochemical similarities of the selected plant species as well as of the invaded plant organs and tissues, certain authors paying more attention to "nutritional" substances, while others to "attractive" substances. Hering's excellent theory (1926, 1951a) establishing a connection between the choice of food by mining insects and the affinity of specific plant proteins is an interpretation of the first kind. Hering starts from the assumption that plant proteins are the main, if not the only, food of mining insects and tries to prove a certain correlation between the oligophagy of these insects and the results of serum diagnoses by the school of Mez. The investigations in question, however, concerned rather relationship between plant families than within them. Thus, it is uncertain, to what extent Hering is justified in establishing some dependence of the food specialization degree of mining insects on that of differentiation of specific proteins of their host plants. Does the monophagy of most miners of the *Ranunculaceae*, *Umbelliferae* and *Compositae* correctly indicate a high degree of protein differentiation within these families? Does the preponderance of oligophagy among miners of the *Caryophyllaceae*, *Cruciferae*, *Rosaceae* and *Gramineae* correctly indicate a low degree of such differentiation? This will perhaps be answered by more detailed serum diagnoses. The behaviour of oligophagous species in cases when serum diagnosis was obviously contrary to the results of comparative morphology and other disciplines which form the basis of systematic botany, would be of the greatest importance in evaluating Hering's theory. In connection with a similar protein reaction of the *Gramineae* and *Leguminosae*, Hering (1951a) indicates that *Domomyza* Rond. is linked exactly with the two unrelated families. It would also be of highest importance to check on some uncertain data concerning *Cerodontha dorsalis* (Loew), a Nearctic species which is said to feed both on the *Gramineae* and on the *Leguminosae* (cf. Venturi, 1946).

It is clear from the view point of Hering's theory that systematic oligophagy must predominate over disjunctive oligophagy, since the affinity of the specific proteins of plants coincides to a large extent with their relationship. However, even if the affinity in question was the main reason for the choice of host plants by oligophagous insects, it would not have to reflect exactly the phyletic relationship of the plants, since it may often be of a symplesiomorphous nature (cf. Hennig, 1957).

The majority of authors seek explanation of oligophagy in the affinity of the plant "attractive" substances. For instance, Fraenkel (1953) maintains that the chemical composition of leaves of Angiosperms as regards substances having nutritional value for insects, amino-acids of proteins included, is of great uniformity. The plants concerned differ rather in "additional" substances

which they contain, such as glucosides, essential oils, alkaloids, sapponines or tannins which though not being proper insect food themselves give it, however, odour and taste. Inducing an attractive or a repulsive effect on phytophagous insects these substances define the host plant specificity. It must be stressed here that the choice of host plants by mining flies is not caused by their smell alone, since the female before oviposition bores with its oviscapt numerous holes in the leaf of the future host plant of the larvae and then sucks its sap with the mouth parts (cf. e. g. HENDEL, 1931; SÉLLIER, 1947; CIAMPOLINI, 1952). Affinity of attractive substances, as rather loosely linked with plant relationship, may be responsible for many a fact of disjunctive oligophagy. Two cases of choice of unrelated host plants containing similar additional substances have been given on page 136: the *Loasaceae* to which *Agromyza reptans* FALL. moves from *Urtica* L. are also provided with stinging hairs and substances. *Tropaeolum* L. which attracts miners of the *Cruciferae*, e. g. *Liriomyza brassicae* (RIL.), contains myrosins and mustard oil glucosides so characteristic for cruciferous plants (cf. BUHR, 1937). However, between *Eupatorium* L. and *Galeopsis* L., both hosts of *Liriomyza eupatorii* (KALT.), no closer phytochemical affinity has been found so far. Though the host plants of every phytophagous species may have or lack certain common chemical substances or certain combinations of them which stimulate the chemoreceptors of the female, the general phytochemical affinity of plants does not always direct their choice.

A certain influence on the choice of host plants, made by phytophagous insect is connected with both their present and original geographic distribution. Distantly related plants but having a coincident or overlapping geographic area may be invaded by the same parasite, not occurring on a plant more closely related to one of them but geographically isolated — even when such a plant subsequently enters that area. Such an omission of an allochthonic plant species, despite its close relationship with some autochthonic host plants, is referred by HERING (1952) as xenophoby (Xenophobie). *Ophiomyia maura* (MEIG.), for instance, living in Europe on *Solidago virgaurea* L. and *Aster amellus* L., and in Japan also on *Erigeron annuus* L. (SASAKAWA, 1953), avoids *Solidago canadensis* L. and *S. serotina* AIT. of North American origin, now common in Europe. *Robinia pseudacacia* L., of North American origin too, is avoided in Europe by oligophagous species feeding on related *Leguminosae*, e. g. by *Liriomyza variegata* (MEIG.) and *L. trifolii* (BURG.), excluding some rare cases of lethal oligophagy of the latter species. It is worthwhile to mention that some restricted xenophoby may also be combined with systematic oligophagy of higher degrees and even with polyphagy. Thus, for examples *Liriomyza brassicae* (RIL.) seems to occur in Central Europe only on weede and cultivated plants of the families *Cruciferae*, *Resedaceae*, *Capparidacea*, and *Tropaeolaceae*; it avoids, on the other hand, many autochthonic cruciferous plants, e. g. of the genera *Cardamine* L., *Dentaria* L., *Rorippa* SCOP.,

Turritis L., *Arabis* L., *Alyssum* L., *Lunaria* L. and others. The author has also observed considerable nonuniformity of distribution of polyphagous species in Poland. Only *Liriomyza strigata* (Meig.) is common in most habitats in the area. The three other polyphagous species, i. e. *Phytomyza atricornis* Meig., *Liriomyza bryoniae* (Kalt.) and *L.* (*Cephalomyza*) *crucifericola* (Her.), occur in greater numbers only in synanthropic and certain anthropogenic habitats, showing some xenophoby towards the autochthonic flora and quite evident attachment to cultivated, weed and meadow plants of foreign origin, which they have probably come with. *Phytomyza atricornis* Meig. seems to occur more frequently on autochthonic plants of the Mediterranean bassin (cf. Hering, 1936). The rarity of this apparently photophilous species in Polish natural forest habitats may be explained not so much by the negative influence exerted by the secondary environment, as by exactly these habitats being the home and refuge of the autochthonic flora. This polyphagous species may penetrate the remote depth of the shadowy forest along weedy paths covered with such plants as *Taraxacum officinale* Web., *Leontodon autumnalis* L., *Sonchus arvensis* L., *Centaurea jacea* L., *C. scabiosa* L., *Capsella bursa-pastoris* (L.) Med. and others.

The phenomenon opposite to xenophoby is xenophily (Xenophilie, Hering, 1952), i. e. favourising of allochthonic plants. This phenomenon has been noticed by Hering (1952) in *Liriomyza impatientis* (Bri.) which was said to occur rather rarely on *Impatiens nolitangere* L., an autochthonic plant growing in shadowy deciduous forests, but in masses on *Impatiens parviflora* D. C., now quite a common weed, a refugee from botanical gardens, brought to Europe from Central Asia. According to the author's observations made at a number of stations in Poland, *Liriomyza impatientis* (Bri.) occurs, however, with equal frequency on its two host plants.

A considerable influence on the plant choice by the insects in question is also exerted by certain morphological and anatomical features of the invaded plant organs, thus, in the first place, of the leaves. This influence is revealed, when the same insect species feeds exclusively on plants with similar leaves but which are not considered as directly related, owing to certain larger differences in the generative organs, or else when an insect species avoids a plant species of a leaf structure not typical for the group of its host plants. *Phytomyza aquilegiae* Hardy and *Ph. minuscula* Gour., for example, feed only on *Aquilegia* L. and *Thalictrum* L. which were included in various tribes of the *Ranunculaceae*, while *Phytomyza tussilaginis* Hend. and *Ph. adenostylis* Her. feed on *Adenostyles* Cass. and *Petasites* Mill. (the former species also on *Tussilago* L.) belonging to different tribes of the *Compositae* (cf. Wettstein, 1933). *Napomyza aconitophila* Hend., *Phytomyza aconiti* Hend. and *Ph. aconitella* Hend. linked with *Aconitum* L. and *Delphinium* L. avoid *Delphinium consolida* L. characterized by thread-like leaf lobes. *Liriomyza variegata* (Meig.) occurs frequently or even in mass on *Astragalus glycyphyllos* L. and *Colutea arborescens*

L. but it is only rarely found on species of *Astragalus* L. with small leaflets. Certain of these cases may result from some imperfection of the existing plant classification. Hering (1957a, 1958a), for instance, is convinced as to a close relationship between *Aquilegia* L. and *Thalictrum* L.; in the modern system of plants it is proposed to include both these genera in the same tribe — *Thalictreae*. The resemblance of the leaf shape as such must be of little importance to phytophagous insects, it may, however, be correlated with certain phytochemical and physiological similarities more essential for them. The examples of xenophagy (in the strict sense) given in the literature (cf. pp. 138—139) seem to us not very convincing for the simple reason that the non-specific host plants usually have leaves very much like those of the specific ones, thus we suspect the authors of the examples may have misidentified the plants. The resemblance of the leaves of *Eupatorium cannabinum* L. to those of *Cannabis sativa* L. — two completely unrelated plants but which are hosts of a sister pair of species, i. e. *Liriomyza eupatorii* (Kalt.) and *L. cannabis* Hend. (cf. pp 136, 138), show probably that these suspicions may not be justified in some cases. On the other hand, however, we do find more often the same or else sibling insect species on related plants, leaves of which differ considerably in shape, size, thickness, venation and pilosity. Occurrence of *Trilobomyza verbasci* (Bché) both in the wooly-pilose leaves of *Verbascum* L. and in the bare leaves of *Scrophularia* L. is held to be a case of such a kind.

What can be observed in most cases is that hard and stiff leaves containing many cells with thickened and sclerotized membranes as well as scalelike or tiny leaves are avoided. This results, in the first place, from the preference of phytophagous dipterous larvae for soft tissues resembling humid and mouldering plant parts, their saprophagous ancestors lived in. Such inclinations have been due to the very structure of the maggot: its thin cuticle, the lack of a head capsule and the rather weak mouth armature. In hard leaves a considerable resistance of the plant tissue is to be overcome by the larva, while in tiny leaves it runs the danger of being dried up; a tiny leaf, after all, usually does not supply food in a sufficient quantity for the full development of the larva. These circumstances seem to be expressed in the attitude of the *Agromyzidae* towards large groups of green land plants. These insects live on Angiosperms and ferns and on liver mosses (*Hepaticae*) with a leaf-shaped thallus. Conifers, with hard and needle-like leaves, as well as club mosses (*Lycopodiinae*) and mosses, with scaly and tiny leaves, are avoided. Only two species feeding inside stems occur on horsetails (*Equisetinae*). From among the Angiosperms which are the main group of hosts of the *Agromyzidae* many xeromorphic plants with cutinized, needle-like or bristle-shaped leaves, are avoided, e. g. in the Polish flora: *Polycnemum* L., *Corispermum* L., *Kochia* Roth. (*Chenopodiaceae*), *Tunica* Boehm., cushionlike species of *Dianthus* L. and *Silene* L., *Heliosperma* Rchb., *Arenaria* L., *Minuartia* L., *Sagina* L., *Scleranthus* L., *Delia* Dum., *Herniaria* L. (*Caryophyllaceae*), *Asarum* L. (*Aristo-*

lochiaceae), *Helianthemum* Mill. (*Cistaceae*), *Dryas* L. (*Rosaceae*), *Eryngium maritimum* L. (*Umbelliferae*), *Armeria* Willd. (*Plumbaginaceae*), the whole order *Bicornes*, *Androsace* L. (*Primulaceae*), *Vinca* L. (*Apocynaceae*), species of *Juncus* L. and *Cyperaceae* with bristle-shaped leaves, *Stipa* L., *Corynephorus* P. B., *Koeleria* Pers., *Nardus* L. (*Gramineae*). Other xeromorphic plants of that kind are invaded rather seldom and if so, then by more polyphagous or not very restricted oligophagous species. The preference of dipterous larvae for soft tissues partly explains their preference for herbaceous plants and dislike for xylophytes, the leaves of which are rather stiff and hard, while their stems are sclerotized and covered with a secondary cortex. Both the arboreous and xeromorphic conifers are completely omitted. It is also very seldom to find dipterous mines on Mediterranean macchia shrubs and generally on xylophytes with evergreen leaves (exceptions: *Ilex* L., *Phillyrea* L., *Eleagnus* L.). Out of all the leaf mining species of the *Agromyzidae* only five per cent live on arboreous Angiosperms, three quarters of which have been connected with shrubs. In addition we know two species groups feeding in the soft meristematic tissue (cambium) between the cortex and xylem of tree and shrub trunks: the group of *Melanagromyza schineri* (Gir.) and the genus *Phytobia* Lioy (= *Dendromyza* Hend.). As regards the scanty Agromyzid species which mine in tree leaves, they invade mostly those of young twigs. This can be best seen in the case of *Agromyza albitarsis* Meig., the mines of which are to be found most frequently on juvenile (heart- or lozenge-like) leaves of *Populus tremula* L. and *P. alba* L., and rarely on circular or lobate ones growing on elder twigs. *Agromyza celtidis* Nowakowski (1960b) feeding merely in young and growing leaves of *Celtis australis* L. is such an example too.

We see that the dependence of choice by phytophagous insects on the structure of invaded plant organs, especially that of leaves, is, at the same time, to a certain extent the dependence on the ecological type and the growth form of the plant. The dependence on the growth form causes a nearly one stratum vertical distribution of the mining flies. This is intensified by the fact that most Agromyzid species mining tree leaves avoid young twigs in the higher crown stratum invading but young trees and lateral shoots or lower twigs of the crowns at most. Such is the behaviour of parasites of willow trees, moreover of *Phytomyza heringiana* Hend. on *Malus silvestris* (L.) Mill., *Agromyza albitarsis* Meig. on *Populus tremula* L. and *P. alba* L., *Agromyza alnibetulae* Hend. on *Betula verrucosa* Ehrh. and *Alnus glutinosa* (L.) Gaertn., and it was only on *Alnus incana* (L.) Mnch. that the author found mines of the latter species also in the tree crowns up to a height of 4 m, just as was the case with mines of *Phytagromyza tremulae* Her. on *Populus tremula* L. Higher in the crowns we have found nothing but mines of *Phytagromyza populi* (Kalt.) and *Ph. populicola* Hal. on *Populus nigra* L. and mines of *Phytagromyza heringi* (Hend.) on *Fraxinus excelsior* L., both trees growing in humid habitats. An obvious predilection of mining flies for the herbaceous vegetation stratum,

their scanty occurrence in the shrub stratum (in the forest undergrowth) and their great rarity in the tree crown stratum, thus results not merely from the inclination to soft plant tissues but also from certain other biotic characters of these tiny insects, such as hygrophily, liking for shadow, flight near the ground and pupation in the soil[1].

Hygrophily and liking for shadow and plant parts having soft tissue are three, to some extent, mutually conditioned, original and predominating ecological inclinations of dipterous mining maggots (cf. NUNBERG, 1947; BEIGER, 1955), linked with their morphological features. These inclinations should result in certain dependence of the host plant choice also on the ecological character of the plants, consisting mainly in some preference for hygrophytes and mesophytes rather than for xerophytes. Indeed such preference exists but it is due to certain morphological features of the xerophytes rather than to their ecological features. The only ecological type of vascular plants that seem to have been completely omitted by the *Agromyzidae*, are exactly certain plants having soft tissues — proper aquatic plants (hydrophytes). This seems to be a typical example of pseudoresistance, i. e. evasion (cf. DETHIER, 1953), since the resistance to parasite invasion is due here not so much to the plant itself as to its environment. A very high percentage of *Agromyzidae* adapted themselves, on the other hand, to xero- and heliophilous land plants living in light and dry forests and on "open stations", such as meadows, fields, steppes etc., since endophagy enables the larvae to exist even in very strong insolation, winds, dry air and on dry soil. It is not so much xerophilous plants, as certain xeromorphic ones that are avoided. On the one side, numerous plants having not too hard and not too tiny leaves living in dry habitats are hosts of *Agromyzidae*[2] and, on the other, the flies avoid the majority of hard or tiny leafed plants in humid habitats. For instance, on southern slopes of the Kampinos-Forest dunes, on which certain plants wither on a hot day and the sand warms up to a temperature of 60°C, the author found larvae in the midsummer, mining in xerophilous plants, e. g. larvae of ***Phytomyza pauliloewi*** HEND. on ***Peucedanum oreoselinum*** (L.) MNCH., ***Liriomyza scorzonerae*** RYD. on ***Scorzonera humilis*** L., ***Phytomyza campanariae*** NOWAK. on ***Pulsatilla pratensis*** (L.) MILL. and others. Much material for HERING's works came from xerothermic banks of the Odra River. Numerous Agromyzid species live on steppe plants, particularly on representatives of the families: ***Compositae***, ***Umbelliferae*** and ***Ranunuculaceae***, growing on soils rich in calcium carbonate and moulder. On the other hand, representatives of the order *Bicornes* (*Vacciniaceae*, *Empetraceae*, *Pirolaceae*) avoided by the *Agromyzidae* are of

[1] Pupation inside the leaf is a secondary habit which has also been aquired by the three mentioned species occurring in the higher crown stratum.

[2] The succulent xerophytes are rather avoided probably because of their water tissue.

a xeromorphic type (cutinized or needle-like leaves, usually evergreen) but grow not so much on dry as on humid or even swampy soils which are physiologically dry for them as a result of their acidity. The plants in question together with conifers, mosses and lichens, predominate in the vegetation of oligotrophic soils, i. e. in acidophilous coniferous forests, on heaths and high peat-bogs. That is why these habitats, despite a frequently high humidity, have an extremely poor fauna of mining flies.

Distribution of the *Agromyzidae* on the Vegetation

If we take into consideration that the choice of a host plant by a phytophagous insect is influenced not only by the systematic position and chemical specificity of the plant but also by certain morphological peculiarities of the invaded plant organs, the growth form and the ecological character of the plant and finally by the secondary environment, we shall be in a position to begin to understand the distribution of the *Agromyzidae* on the vegetation, their horizontal and vertical distribution, in habitats and in geographic regions. In natural conditions the fauna of the flies concerned depends, in the first place, on the trophic conditions of the soil, not only since eutrophic soils nourish a rich flora and abundant vegetation, and oligotrophic soils only a monotonous flora and poorer vegetation, but also because the latter supports mostly xeromorphic plants. Moreover, humid habitats (i. e. having moist air and soil) must have a superiority over dry ones, not only because the tiny flies are hygrophilous but mainly due to the flora and vegetation of the dry habitats being usually poorer and having a higher percentage of xeromorphic plants. A temporary flood of the soil surface, however, brings about unfavourable conditions for the pupation of the larvae and the emergence of the adults. Shadowy habitats (lower forest strata) are privileged as compared with open habitats (upper forest strata and the so-called "open spaces", particularly those with a low and scanty vegetation). On the other hand, strong tree shadow impoverishing the herbaceous ground covering plays a negative part. Due to dampness, shadow and protection from winds a forest must be, as a rule, a more favourable habitat than is the case with "open spaces", but it is only so when the herbaceous vegetation stratum is well developed. A higher percentage of arboreous plants in the flora and vegetation impoverishes the fauna of mining flies. This will be well illustrated by comparing the Agromyzid faunas of five typical forest communities of the Polish lowland, occurring in the Kampinos-Forest near Warszawa[1].

[1] The Kampinos-Forest is considered here historically as a whole, together with remnants of forests on the Vistula flood terrace. The phytosociological classification of the natural plant communities has been carried out on the basis of the papers of Matuszkiewicz and of his school (1952, 1955, 1957, 1958).

1) Willow-poplar forest (Saliceto-Populetum). Habitat with eutrophic soil, very humid, shadowy, rich in floristic composition, thickly forested and with deciduous undergrowth, with high and thick ground covering consisting of hygrophytes and mesophytes. The ground covering has been partly impoverished or even completely driven out due to considerable bush thicket and shadow. The soil is damp, periodically watered by river floods. — The Agromyzid fauna is here in its best both in the quantitative and qualitative aspects (as estimated per unit of surface), represented still in fair numbers in the undergrowth stratum — on climbers (*Humulus lupulus* L.), shrubs (*Salix* L., *Sambucus nigra* L., *Cornus sanguinea* L.), on young trees and lateral shoots of old ones [*Salix alba* L., *Populus nigra* L., *P. alba* L., *P. tremula* L., *Alnus incana* (L.) MNCH.], occurs also in the crown stratum (on *Populus nigra* L.)[1]. In places where the ground covering is thinning or when it is flooded the fauna has been found much poorer. Generally speaking, the further from the river bed, the more favourable are here the conditions, an optimum being reached in the more arid parts of the forest.

2) Oak-hornbeam forest (Querceto-Carpinetum medioeuropaeum). Habitat with mesotrophic soil, humid, usually very shadowy, rather rich in floristic composition, consisting mostly of deciduous trees, a thick deciduous undergrowth, and a ground covering consisting mainly of mesophytes but with an admixture of xerophytes. Here and there, due to strong shadow both in summer and autumn, the ground covering has been thinned and regenerates only in spring. — The Agromyzid fauna is in general abundant, represented still in the undergrowth too [on *Cornus sanguinea* L., *Malus silvestris* (L.) MILL., *Betula verrucosa* EHRH., *Populus tremula* L.]. But in places having thin ground covering, the fauna has been found to be either poor or very poor.

3) Mixed pine-oak forest (Pineto-Quercetum). Habitat with mesotrophic soil but tending towards oligotrophy, moderately humid or dry, rather light, rich in floristic composition, with coniferous-deciduous trees and undergrowth, having abundant ground covering constisting mainly of xerophytes (elements of acidophilous pine forest, basophilous oak forest and psamnophytes), with an addition of mesophytes of the oak-hornbeam forest. — The Agromyzid fauna rich qualitatively as a whole (i. e. large number of species found in all the areas investigated) but when estimated per unit or surface, looks rather poor, both in quantitative and qualitative aspects, and is poorly represented in the undergrowth.

4) Typical pine forest (Myrtillo-Pinetum s. l). Habitat with oligotrophic soil, either dry or very dry (Cladonio-Pinetum), light, poor in floristic composition, with coniferous trees, thin coniferous-deciduous undergrowth and a low ground covering consisting of xerophytes (elements of acidophilous pine forests

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[1] In crowns of *Fraxinus excelsior* L. the author has found mines in an alder-ash swampy forest on the dune terrace of the Kampinos-Forest (at Karolinów, on 23 X 1957).

and psammophilous ones). — The Agromyzid fauna very poor, connected rather with plants occurring more abundantly on mesotrophic soils [*Solidago virgaurea* L., *Peucedanum oreoselinum* (L.) MNCH., *Pulsatilla pratensis* (L.) MILL., *Scorzonera humilis* L., *Silene nutans* L.], and with psammophytes (*Hieracium pilosella* L., *Jasione montana* L.), hardly represented in the undergrowth (only on *Betula verrucosa* EHRH.).

5) Swampy pine forest (Uliginoso-Pinetum). Habitat with oligotrophic soil, humid, light, poor in floristic composition, with coniferous trees, a thin coniferous-deciduous undergrowth, and a tufty ground covering consisting mainly of xerophytes (elements of acidophilous pine forest and sphagnous ones). Swampy soil. — The Agromyzid fauna very poor, connected rather with plants of the mixed pine-oak forest or of Saliceto-Franguletum, such as *Potentilla erecta* (L.) HAMPE, *Molinia coerulea* (L.) MNCH., *Peucedanum palustre* (L.) MNCH., *Comarum palustre* L., hardly represented in the undergrowth (but rarely on *Betula verrucosa* EHRH.).

In the investigated area of sphagnous pine forest (Pineto-Sphagnetum, KOBENDZA, 1930) forming an intermediate link with high peat-bog (Sphagnetum pinetosum, MATUSZKIEWICZ, 1952) no Agromyzids have benn found by the author. On typical high peat-bogs there exists probably some fauna connected with low peat-bog elements predominating at the bog edges. On sphagnous vegetation some species of unknown ecology have been captured too, e. g. *Encoelocera bicolor* LOEW (HERING, cf. FRICK, 1952) or *Phytagromyza incognita* HER. (cf. HERING, 1956a).

A strong impoverishment of the Agromyzid fauna is a significant fact when passing from a habitat with mesotrophic soil to one with oligotrophic soil; this is caused by food conditions, namely a lack of almost all species of host plants. Among plant species characteristic for communities connected with oligotrophic soils and among species predominating in these communities there are only very few hosts of mining flies, and the hosts in question seem to be invaded here with a lesser intensity than in communities on more fertile soils. In line with the "law of minimum", increase in humidity of a habitat having a poor and acid soil is in no way advantageous for the flora and fauna but, on the contrary, the flora and fauna become still poorer due to the swamping of the soil.

If, according to the data known so far, the area of the most abundant occurrence of *Agromyzidae* in Europe is the zone of mixed and deciduous forests, this is so not only due to the better state of investigation of this zone. Both in the taiga an tundra zones as well as in the steppe or the Mediterranean zones the fauna of these flies should be poorer in general due to preponderance of xeromorphic vegetation. In the northern coniferous forest zone (taiga) as well as the northern treeless zone (tundra) there prevails a monotonous acidophilous and sphagnous vegetation, hygro- and mesophytes being distributed rather along rivers only. An estimate made by RYDÉN (1954) has shown

that the Agromyzid fauna of Sweden is richest in the southern part of the country, which still belongs to the mixed forest zone. In the north the number of species declines, the lowest being in Lappmark belonging partly to the tundra zone. The cooling of the climate itself should play no decisive part here, for mining flies are rather resistant to low temperatures. This can be proved by the fact that many larvae feed late in autumn and certain species in winter too [e. g. *Phytomyza ranunculi* (SCHRK.), *Ph. ilicis* CURT., *Ph. hellebori* KALT., *Ph. anthrisci* HEND.], or else early in spring — under the snow (e. g. *Phytomyza abdominalis* ZETT. on *Hepatica nobilis* GRSL.), as well as the fact that many species occur above the upper forest limit in subalpine and alpine zones. The Mediterranean vegetation is characterized by a higher percentage of arboreous plants and preponderance of evergreen plants, with cutinized or tiny leaves often even transformed into thorns or else althogether reduced. That is why, as far as the Mediterranean flora is concerned, the fauna of mining flies is relatively rather poor (cf. HERING, 1936, 1943).

Similar relations can be seen when investigating the Agromyzid fauna on the vegetation of the mountains (e. g. Tatra). The optimal habitat here is the beech-fir forest in the lower forest zone (Fagetum carpathicum), resembling in its ecology the oak-hornbeam forest but still damper, having a richer flora, particularly in light penetrated places, on the outskirts of forest clearings; the optimal constitute also plant communities along stream banks and communities of high herbs (Adenostylion alliariae) in the whole mountain forest zone. The monotonous spruce forest in the upper forest zone (Piceetum tatricum) is a humid habitat with an oligotrophic soil, though enriched, particularly on calcareous substratum, with certain montane elements which the swampy and typical pine forests lack in lowlands. Above the upper forest limit there prevail not only unfavourable climatic conditions (humidity and temperature fluctuations, strong insolation and winds) but also xeromorphic plants, particularly with tiny leaves. That is the reason why the Agromyzid fauna can hardly equal the abundant alpine flora, though it reaches the highest peaks of the Tatra Mountains [e. g. *Phytomyza aronici* NOWAK. (in course of description) and *Ph. atricornis* MEIG. on *Doronicum clusii* ALL. TAUSCH, *Napomyza gentii* HEND. on *Gentiana punctata* L., *Phytomyza mutellinae* BEIGER on *Mutellina purpurea* (POIR.) THELL. and *Pachypleurum simplex* (L.) KOCH].

Taking into consideration the influence of some ecological and morphological peculiarities of the plant as well as the factors of soil and climate of the secondary environment on the plant choice by phytophagous insects, we must bear in mind, however, that the factors in question merely modify the significance of the most important factor, i. e. the systematic position of the plant. The habits of the oligophagous *Agromyza spiraeae* KALT. well illustrate this principle. Its primary host plant seems to be *Filipendula ulmaria* (L.) MAX., an eutrophic hygrophyte readily invaded in swampy forests, such as flooded or typical alder forests, rather than on swampy meadows.

The insect in question occurs frequently also on *Geum rivale* L. and *G. urbanum* L., particularly in humid thickets and forests and also on *Rubus idaeus* L. known for its eutrophism, not so often on *Rubus caesius* L., and quite exceptionally on the shrubby blackberry (*Rubus fruticosus* L. s. l.) with harder leaves, particularly when growing in dry habitats, e. g. on sandy road-sides. Shrubby roses (*Rosa* L.) are not its favourites either. In swampy forests and bushes we find its mines on *Comarum palustre* L., in humid coniferous forests and thickets on *Potentilla erecta* (L.) Hampe and *P. reptans* L., in shadowy places or in autumn also on certain meadow plants, e. g. on *Potentilla anserina* L., while hardly they are found on the xerophilous species of *Potentilla* L., such as *P. argentea* L., *P. alba* L. or *P. arenaria* Borkh. growing on sands. On *Fragaria* L., *Agrimonia eupatoria* L. and *Filipendula hexapetala* Gilib. mines were found in damper and shadowy places or in autumn only. Neither is *Sanguisorba* L. favoured because its leaves are hard. In the mountain forest zone *Geum rivale* L., *Rubus idaeus* L. and even meadow species of *Alchemilla* L. are invaded. Above the upper limit of the forest zone no mines of *Agromyza spiraeae* Kalt. have been found by the author either on *Geum montanum* L. or on *G. reptans* L., this being considered as due to pseudoresistance, or on *Dryas octopetala* L., what can also be due to its leaves being stiff and cutinized. Thus, we see that an inclination for eutrophic plants having soft leaves, hygrophily and liking for shadow by *Agromyza spiraeae* Kalt. is expressed in choice of both the host plants and habitats. The selection concerned, however, is effected within strict limits of a systematic group of host plants, namely the subfamily *Rosoideae*.

A number of Agromyzid species feed both in the lowlands and the mountain zone and even in the alpine zone, e. g. *Phytomyza gentianae* Hend. connected with *Gentiana* L. and *Centaurium* Hill., *Ph. swertiae* Her. known till now only from the lowland (nominal) subspecies of *Sweertia perennis* L. and found by the author in the Tatra Mountains on *S. perennis* ssp. *alpestris* (Bmg.) Jav. (2 ♂♂ reared on 4 III 1958 from larvae collected in the valley Białego on 26 VIII 1957), *Ph. virgaureae* Her. found by the author also in the Tatra on *Solidago virgaurea* ssp. *alpestris* (W. K.) Gaud. (1 ♀ reared on 11 III 1958 from a larva collected near the lake Morskie Oko on 3 IX 1957), *Ph. senecionis* Kalt. common in mountains on *Senecio fuchsii* Gmel., *S. nemorensis* L. and *S. subalpinus* Koch. and found by the author on *S. fluviatilis* Wallr.[1] on the Vistula flooded terrace (1 ♀ reared on 1 VII 1954 from a larva collected at Młociny near Warszawa on 13 VI 1954, numeorous larvae found also in Mątowski Forest near Sztum in Polish Pomerania on 25 IX 1960), *Ph. klimeschi* Her. found by Hering in the Alps on *Achillea clavenae* L. and *A. moschata* Wulf. and by the author in the Polish lowland (Kampinos-Forest) on *A. millefolium* L. (1 ♂ reared on 9 VIII 1955 from a larva collected at Cisowe

[1] *Senecio jacobea* L. seems to be only an occasional host plant of *Ph. senecionis* Kalt.

on 21 VII 1955, 2 ♂♂ and 1 ♀ reared on 14 X 1955 from larvae collected at Młociny on 25 IX 1955 and 1 ♀ reared on 7 VIII 1957 from a larva collected at Cybulice on 19 VII 1957). The *Agromyzidae* are rather faithfully attached to their primary (main) host plants and in accompanying them they show much tolerance as regards their secondary environment. If a given Agromyzid species has been already found to occur in a certain locality, it is likely to occur everywhere its primary host plants grow, unfavourable conditions prevailing in some habitats or stations do nothing more than limit its frequency without excluding its actual presence. At times, however, for unknown reasons some Agromyzid species are absent in certain geographic areas or localities, despite the presence of their primary host plants. The Kampinos-Forest is in general poor in Agromyzids, because of a preponderance of dry and oligotrophic habitats. The author has, however, found there an overwhelming majority of leaf mining species of *Agromyzidae* recorded from Central Europe on the plants occuring also in this Forest. The author has even found certain monophagous or limited oligophagous species to be present here on plants which are already or still very rare in the Forest, e. g. *Phytomyza digitalis* Her. on *Digitalis grandiflora* Mill. (1 ♂ reared on 5 VIII 1956 and 1 ♀ — on 22 IV 1957 from larvae collected at Cybulice on 8 VII 1956), *Phytomyza actaeae* Hend. on *Cimicifuga europaea* L. (15 ♂♂ and 14 ♀♀ reared on 10—20 VIII 1956 from larvae collected at Cybulice on 24 VII 1956), *Phytomyza lithospermi* Nowak. on *Lithospermum officinale* L. (cf. Nowakowski, 1959). In spite, however, of intensively conducted field work he has failed to find parasites of certain plants occuring in the Forest, though he has very often found these parasites on the very same plants in Polish Pomerania (Isle of Wolin and Kashubian Switzerland) and in the forest zone of the Carpathian and Sudety Mountains; such are e. g. *Phytomyza sonchi* R. D. on *Liguliflorae*, *Ph. taraxaci* Hend. on *Taracacum* Zinn, *Ph. minuscula* Gour. on *Aquilegia* L. and *Thalictrum* L., *Ph. tussilaginis* Hend. and *Ph. farfarae* Hend. on *Tussilago farfara* L., *Liriomyza* (*Praspedomyza*) *approximata* (Hend.) on *Daphne mezereum* L. Certain Agromyzid species have been, despite their host plants being common, so rare in the Kampinos-Forest, that they have not been found but until recently after many a year of work, e. g. *Metopomyza violiphaga* (Hend.) on *Viola* L. (empty mines on *V. silvestris* Rchb. found at Głusk on 25 VII 1957). These facts prove that the distribution of the *Agromyzidae* depends in the first place on the flora and vegetation, but not exclusively.

Connection of Food Specialization with Speciation

The systematic oligophagy of species has to a certain extent its equivalent, at the level of higher taxonomic units in a phenomenon also spread among phytophagous insects and predominating in the group of miners discussed — the phenomenon of occurrence of related insect species on related groups of

plant species. The relations in question are not clear until the artificial system is replaced by the natural one (cf. pp. 96—107). The rank of supraspecific units both of animals and plants is determined, to a large extent, in an arbitrary way. Nevertheless, if as far as possible a uniform classification is maintained, we shall see that the natural genera of *Agromyzidae* are usually linked with families, orders or groups of related orders of host plants. While among the Agromyzid species prevails monophagy of the second and third degrees, rather restricted systematic oligophagy of the first degree also being frequent, wide systematic oligophagy of the first, second and third degrees seems to prevail among the natural genera. Oligophagy of the first degree corresponds to the feeding habit of e. g. *Phytagromyza* Hend. (on *Salicaceae*), the group of *Agromyza ambigua* Fall. (on *Gramineae*), of *Phytomyza obscurella* Fall. (on *Umbelliferae*), of *Ph. obscura* Hend. (on *Labiatae*), oligophagy of the second degree — to the feeding habit of e. g. *Rubiomyza* gen. nov. (on *Rubiales*), oligophagy of the third degree — of e. g. *Cerodontha* Rond. (on *Glumiflorae*, *Cyperales* and *Liliiflorae*). Thus, in many cases natural Agromyzid genera or subgenera represent a degree of systematic oligophagy, immediately higher than that represented by the species they consist of. Deviations from the governing principle of systematic oligophagy are met, however, far more frequently and extensively at the level of genera or groups of related genera than at that of species. Disjunctive or combined oligophagy corresponds to feeding habits of e. g. *Phytobia* Lioy (on *Salicaceae*, *Betulaceae* and *Rosaceae*), *Trilobomyza* Hend. (on *Centrospermae* and *Tubiflorae*), of the complex of *Phytomyza albiceps* Meig. (on *Compositae* and *Umbelliferae*). Combined oligophagy on the level of a natural supraspecific unit corresponds to the phenomenon known in parasitology as "desertion" consisting in one or a few representatives of a parasitic group occurring on some entirely different group of hosts than the overwhelming majority of the parasitic group in question. For example, *Phytomyza brischkei* Hend. living lonely on *Trifolium* L. (*Leguminosae*) is closely related to the group of *Phytomyza rectae* Hend. linked with *Ranunculaceae*. The facts mentioned show that various kinds of "phagism", and particularly various degrees of systematic oligophagy (in the broad sense), are in a close and reversible relation with each other.

Restriction of the range of specific host plants, called in the case of phytophagous insects "food specialization", is a kind of physiological and ecological specialization which, as is the case with morphological specialization, we recognize to be the chief trend of evolution, one of its fundamental "principles". That is why the majority of authors believe that monophagy is secondary to polyphagy and that monophagy has developed from polyphagy via oligophagy (cf. Petersen, 1930; Brues, 1946; Allee, 1949; Hering, 1951a). At the same time, however, these authors assume the shifting of phytophagous insects to secondary host plants, i. e. widening of the host range (Wirtskreiserweiterung) which is in accordance with the general biological principle

of extension of the living space. Theresult of this expansion is a certain temporary despecialization, some extension of the ecological niche, passing from monophagy to oligophagy or even to polyphagy. Some extension of the host range, however, causes in turn differentiation of new parasitic species, hence the expansion brings a secondary specialization and narrowing of the ecological niche. Phytophagous species have a certain ability to expand to new host plants but, at the same time, tend towards monophagy. Monophagy is advantageous for the species, because it ensures a more stable equilibrium through uniformity of the ecological niche (food uniformity, cf. PETERSEN, 1930). Thus, specialization and despecialization are two opposing tendencies gaining alternatively preponderance in the course of evolution, finally, however, the process of specialization prevails.

HERING (1951) believes that primitive polyphagy gave way to such specialized feeding habit as leaf mining. Present polyphagy of some leaf mining insects is taken to be quite a recent step backwards. Among the *Agromyzidae* polyphagous species show rather a certain preponderance of apomorphy and belong to the "highest" species groups. *Phytomyza atricornis* MEIG. which has the widest host range is simultaneously the most apomorphous among the polyphagous species, and even in a certain respect biotically specialized (the larva pupates inside the leaf in the cradle). *Liriomyza strigata* (MEIG.) would seem biotically primitive, if the leaf mine had been derived from feeding in the stem, because the mine of this species is spread out like a "dendronome", the axis of which is usually the middle rib of the leaf. The larvae are able to move from one leaf to another through the leaf petioles and the stem. This species is, however, as far its male copulatory apparatus is concerned, closely related to the obviously secondary polyphagous *Liriomyza bryoniae* (KALT.) and the monophagous *L. umbilici* HER. In *Liriomyza* (*Cephalomyza*) *crucifericola* (HER.) the clearly apomorphous feature is the lack of acrostichal hairs (*acr*).

A plain inequality of distribution on the flora and vegetation, many taxonomic and ecological plant groups being avoided, while others being preferred — most probably as original host plants — points to polyphagy as secondary for the species mentioned. *Phytomyza atricornis* MEIG. and *Liriomyza strigata* (MEIG.) feed most readily on *Compositae*, *Liriomyza bryoniae* (KALT.) — on *Solanaceae*, *Cephalomyza crucifericola* HER. — on *Cruciferae*. As it has been mentioned, polyphagous species [excluding *Liriomyza strigata* (MEIG.)] occur mainly on synanthropic and allochthonic plants and reveal a certain xenophoby towards the native Central European flora, whence their rarity in many natural plant communities (cf. p. 144). The comparative rarity of *Liriomyza bryoniae* (KALT.) is shown by the fact that until recently it was considered [under the name of *Liriomyza solani* (MACQ.)] as an oligophagous species attached only to the family *Solanaceae*. *Liriomyza* (*Cephalomyza*) *crucifericola* (HER.) has long passed unnoticed due to its resemblance in mines to *Scaptomyza graminum* FALL. and *S. flaveola* MEIG. — two representatives of the

Drosophilids, common on *Cruciferae* and *Leguminosae*. In the Palaeartic Region *Phytomyza atricornis* Meig. is known from as many as over 300 species of Angiosperms belonging to 30 families, and in spite of this it is unlikely to be found in many habitats. Its cosmopolitism is not much the result of its polyphagy alone, as of its inclination to the synanthropic flora. We think that *Phytomyza atricornis* Meig. was originally an oligophagous species feeding on certain *Compositae* (probably *Sonchus* L. and *Taraxacum* L.). When the plants in question were spread outside their homeland, the parasite, as if losing its equilibrium state, turned to polyphagy, thus invading mainly weed and cultivated plants and also wild *Compositae*. A considerable variability of the male genital apparatus, certain external morphological features (either presence or lack of *acr*) as well as puparia and mines of *Phytomyza atricornis* Meig. show a secondary food specialization, i. e. the polyphagous species either losing or having already lost a number of oligophagous and monophagous races (as Hennig, 1950, was correct in supposing).

The problem of passing of phytophagous insects to non-specific host plants has already been dealt with when xenophagy was discussed (pp. 139—140). There exists an expansion to related plants or at least to those which are phytochemically similar (as regards their specific proteins or attractive substances). The choice of a non-specific host plant is, as a rule, taken to be the so-called passive selection caused by a lack of the specific host plant (cf. Dethier, 1953) and to result from (either active or passive) migration to geographical areas situated outside that of the specific host plant, or from plant migrations into new lands (Brues, 1946) or else from violent changes in the vegetation, caused by man, particularly in cultivated territories (Voigt, 1932). Leaps over to secondary host plants have been observed, however, in the vicinity of the primary host too, particularly in botanical gardens (cf. Buhr, 1932, 1937, 1941, 1954). The ability of a phytophagous species to expand may increase with a rapid change of environmental conditions and with its mass occurence — resulting from a shortage of its actual food which is otherwise normally in overplenty, regarding the needs of phytophagous insects. In the Kampinos-Forest, for example, the author was always observing a numerous occurence of *Phytomyza pauliloewi* Hend. on *Peucedanum oreoselinum* (L.) Mnch. but he has not succeeded in finding the insect there, even once, on *Pimpinella saxifraga* L. growing next to its primary host plant in mixed pine-oak, oak-hornbeam and basophilous oak forests. Hering (in litt.) observed *Phytomyza pauliloewi* Hend. to pass over to *Pimpinella* L. in cases of its mass occurence on *Peucedanum oreoselinum* (L.) Mnch.

In view of some facts of secondary polyphagy, combined oligophagy and desertion we have to face the problem of leaps over to plants which are neither taxonomically related nor similar phytochemically. Not all the wide disjunctions in known host ranges prove that such distant transitions have been effected. Disjunctions may also result from former (though secondary) polyphagy,

or they may prove to be alleged after some missing links in the host ranges have been found in the so far uninvestigated geographic areas. Here, the theory of bridging species should be mentioned too; these are plant species or groups of species having some common characters with two unrelated host plant groups; they make it possible to exchange parasitic faunas allied with the groups. *Tropaeolum* L., for example, seems to represent such a bridge between the *Rhoeadales* and the *Leguminosae*, which could have been crossed not only by the leaf mining *Drosophilidae* (*Scaptomyza graminum* Fall. and *S. flaveola* Meig.; Hering, 1951a) but also by certain *Agromyzidae*, e. g. *Liriomyza* (*Cephalomyza*) *crucifericola* (Her.). The problem of direct and distant leaps is more difficult, as we do not trust completely cases of xenophagy (in the strict sense) mentioned in the literature. Voigt (1932) gives two contradictory interpretations of xenophagy of this kind: the female feeling the need for oviposition lays eggs on a non-specific host plant either because she is unable to find the specific one or because she is in the vicinity of the latter and, is mislead by its odour. With reference to the *Agromyzidae* none of the above interpretations seems to be convincing. Where there is a lack of the specific host plants, there should be found some plants related to them. The possibility of mistakes in the choice of the host plant should be rather excluded, since before oviposition the female makes a rather long inspection of the plant and tastes its sap. But if there can be exceptional cases of oviposition on quite a strange plant, the probability that the larvae will survive in this plant is very small. In transplantation experiments made by Buhr (1937, 1954) Agromyzid larvae transferred to plants neither related nor similar phytochemically died before their full development had been achieved [except the disjunctively oligophagous *Liriomyza eupatorii* (Kalt.) and the deserter, *L. cannabis* Hend. (cf. p. 138)]. Finally, even a survival of the larvae and their pupation does not yet mean that they will transform into fertile adults of both sexes and produce a fertile offspring bearing inclination towards the new host plant. Thus, a distant leap must be a consequence of changes in both the instincts and the physiology of a larger number of individuals, a result of their acquiring of an inclination to the new host plant and an ability to overcome its resistance. Such mutations may occur, particularly with some "loosening of heredity" of phytophagous insects in connection with violent changes of environmental conditions.

Splitting of a parasitic species having a larger number of hosts into parasitic species with a smaller number of hosts, either direct or preceded by a transition to the new host, seems to be the most common kind of speciation in the *Agromyzidae*. Divergency of morphological characters is here clearly linked with ecological, ethological and physiological adaptation to different host plants, i. e. with "food specialization". We believe that the splitting of an interbreeding community is effected through the so-called biological races, i. e. ecological races (all kinds of infraspecies, including subspecies) attached

to particular hosts (host races, Mayr, 1953). The problem of these races in phytophagous insects has been discussed mainly by Thorpe (1930, 1940, 1945) and also taken into account by Petersen (1930), Brues (1946), Mayr (1942, 1953), Huxley (1942), Hennig (1950), Barnes (1953) and others. The origin of these races may be explained by Hopkin's host selection principle, according to which polyphagous insect and nematod offsprings usually choose the same species of host plant their parents have developed on. Brues (1946) believes that the female insect usually lays eggs on the same plant species or even variety she has fed on in her larval stage. The biological race, also referred to as "conditioning race", develops gradually from a vague tendency and predilection in a population to a subspecies which is, at the same time, an incipient species. A gradually deepening reproductive isolation of races is caused, in the first place, by zoopsychological (ethological) restrains. Petersen (1930) explains sexual alienation (Entfremdung) of biological races of mining moths by differences in odour. A moth follows the odour not merely when choosing the object for oviposition (food for larvae) but also when choosing a partner for copulation, and the odour of an adult is directly influenced by the host plant (food) of the larva. Consequently, copulating insects are, in the first place, those the larvae of which have fed on the same plant species or even variety. Larval feeding on different host plants reduces sexual contacts of the adults. Petersen believes that a change of food with the insect passing to some other plant may exert an influence through the cytoplasm on the chromosomes of sexual cells, as a mutagenic factor. According to Thorpe (1945), however, the accustoming of individuals to a new host plant is of a rather phenotypic character in its original stage, it is a lasting modification; in turn, due to mutations being parallel to this modification and by the operation of natural selection, it becomes a hereditary one. In this way, structural differences, the increase of which accompanies that of physiological differences may be originally of a phenotypic character too. That is why, while according to the "splitters" the slightest morphological differentiation of the forms attached to various host plants shows peculiarity of ecological niches and lack of interbreeding, the "lumpers" are inclined to see in the differentiation nothing but a reaction of phytophagous species to living conditions in various "primary environments" provided by different host plants. The existence of such ecophenotypes (host determined variations, Mayr, 1953) may be proved only by experiments consisting in transplantation of a parasite from its host to an other. Among phytophagous insects rather few ecophenotypes are known so far, which are clearly differentiated in characters of an apparent taxonomic value. Certain examples have been mentioned by Mayr (1953) and Barnes (1953). We believe that it is rather only in the case when the copulatory apparatus lacks in differentiation that the possibility of ecophenotypes must be taken into consideration, since the deviations in the structure of these organs

are considered to be a barrier separating species or at least populations hereditarily differentiated from each other (cf. pp. 91—92).

The problem of biological races is linked with that of "sympatric speciation", i. e. the origin of species from races that have not been separated by geographical barriers. Authors favouring the concept of sympatric speciation (e. g. HENNIG, 1950) are inclined to hold, usually, that distinguishing early stages of the process as ecological races or subspecies, or else as species is rather an arbitrary or conventional procedure, treated differently by the splitters and the lumpers. MAYR (1942, 1947, 1953), on the other hand, as an opponent of the sympatric speciation concept tries to prove that the supposed "ecological races" which have never been separated by geographical barriers should turn out to be either sibling species, or ecophenotypes, or groups of convergent populations. "No 'ecological races' that are not at least 'microgeographical' too, are known" (MAYR, 1947). MAYR thinks that treating the structurally not clearly differentiated interbreeding communities as races may result from the morphological conception of species being favoured. Nevertheless, even MAYR, while irrefutably denying the species-generating part played by sympatric "habitat races" depending rather on abiotic factors, is inclined to make an exception for the "biological races" of parasites of animals and plants, i. e. for ecological races strictly adapted to some biotic factors, in that case to the particular hosts. For such races may be compared to microgeographic ones due to certain space (topographic) isolation. MAYR, however, stipulates the possibility of existence of these biological races only in parasites which do not change hosts, and the sexual reproduction of which is effected on or in the host. According to BRUES (1946) and certain other authors, biological isolation of host specialized phytophagous insects may have the same effect as geographic separation, for their contacts, particularly in case of feebly vagil forms, are most frequently linked with the food plant. Such an opinion may be valid for the group of mining flies in question since their adults, though gifted with ability to fly keep near their host plants, they are most frequently found on, particularly at their reproduction period. Such a mechanism of biological isolation does not operate, however, in a perfect way, particularly in cases when biological races are not habitat races at the same time, i. e. when their host plants live in similar biotopes. That is why the decisive part should be played here by mechanisms of ethological isolation mentioned already which would at some time be combined with shifts in the season of reproduction (cyclic or phenological isolation) as well as with deviation in structure of the copulatory apparatus (mechanical isolation).

MAYR (1942, 1947) considers the problem of sympatric speciation of parasites to be open and hopes that a further accumulation of examples of such a species-formation will lead to a more accurate analysis of the problem. In this connection, we wish to state that according to the natural system of the *Agromyzidae* the most close related sympatric forms occur usually on different but rather

closely related host plants and have all the character of ecological ("biological") vicariants. The degree of divergency of these forms varies considerably and frequently approaches the invisible spectrum limit of morphological differences.

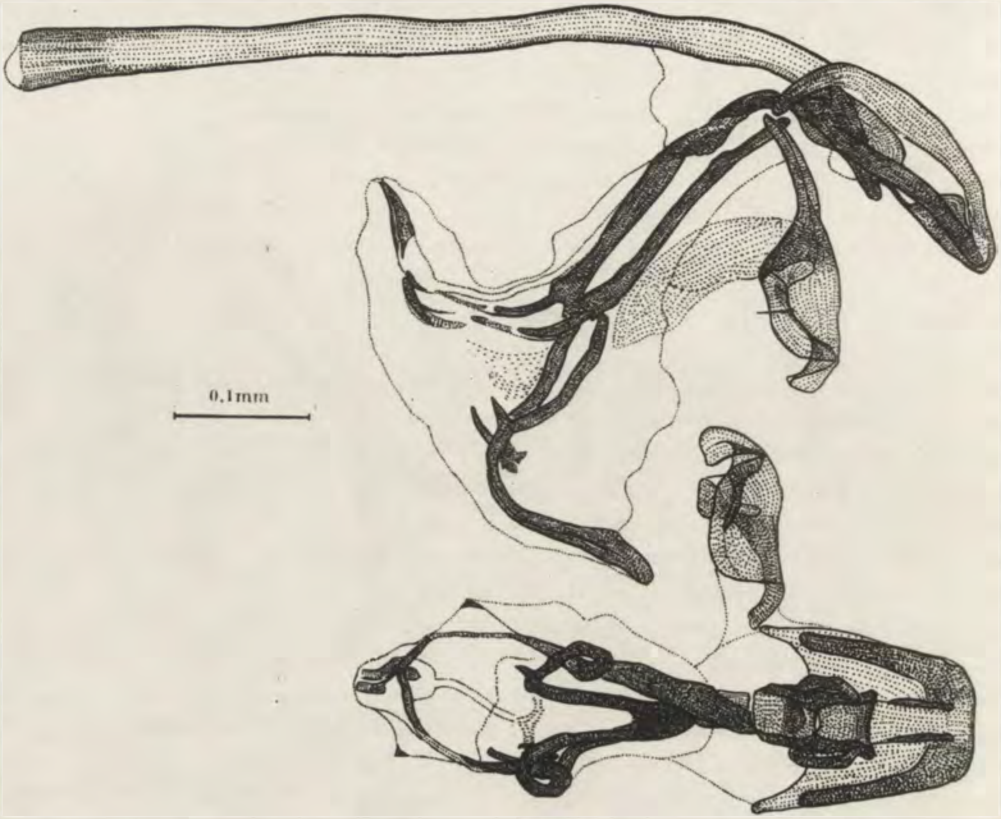


Fig. 68—69. A pair of monophagous sibling species — biological vicariants. Male copulatory apparatus of: 68—*Phytomyza tanaceti* HEND. (from *Tanacetum vulgare* L., Krosno Nadodrzańskie, 24 VI 1931, leg. M. HERING).

Distinction of biological races (incipient species) from the already formed sibling species would in most cases be possible if more subtle methods of examination were applied. When, however, the usual comparative and descriptive methods are used and when a limited material of reared specimens is studied, quite often — in spite of a rather many-sided approach — we can hardly be assured of the taxonomic rank of the biological vicariants examined. On page 114 we have given some examples of "mine-species" between which we have not yet found any constant structural differences, leaving alone the differences

in their variability ranges. These forms are possibly biological races. The genitalia in not all the subspecies of *Phytomyza rectae* HEND. and *Ph. sonchi* R. D., distinguished by HERING (1935–1937, 1957a) are known so far, while we proved the proposed subspecies of *Phytomyza obscura* HEND. to be distinct species (cf. NOWAKOWSKI, 1959). Those biological vicariants which show even the slightest but constant and perceptible structural differences are treated

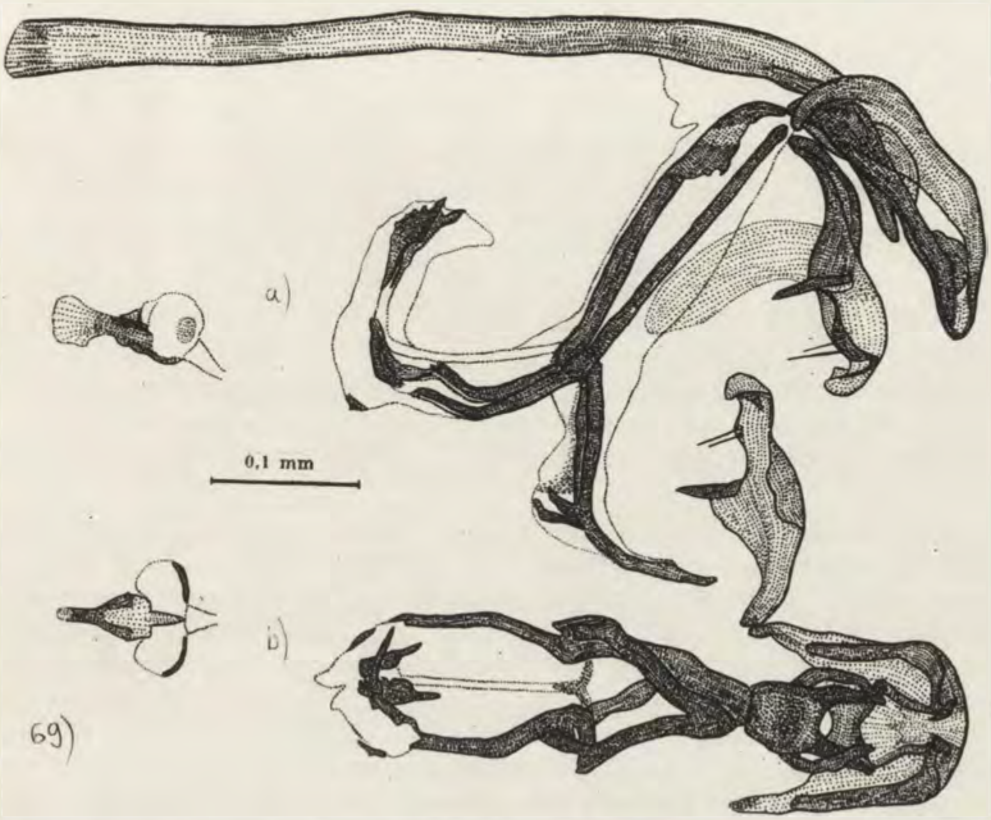


Fig. 68–69. A pair of monophagous sibling species – biological vicariants. Male copulatory apparatus of: 69 – *Phytomyza klimeschi* HER. (from *Achillea millefolium* L., Mlociny at Warszawa, 14 X 1955, leg. J. T. NOWAKOWSKI).

by us as sibling species. The notion is applied here particularly to cover forms externally almost undifferentiated in the adult stage but showing slight but distinct deviations in the structure of their genital apparatus and usually in that of the larva and its mine. Species of this kind are quite common, and their examination makes it possible do detect quite recent traces of speciation. Below we give examples chosen from groups of sibling species adapted to various host plants:

Cerodontha (Dizygomyza) luctuosa (Meig.) (on *Carex* L.), *C. (D) effusi* Karl (on *Juncus effusus* L.) [Fig. 66—67].

Liriomyza pusilla (Meig.) (on *Hieracium* L.), *L. taraxaci* Her. (on *Taraxacum* Zinn and *Leontodon* L.), *L. sonchi* Hend. (on *Sonchus* L.), *L. scorzonerae* Ryd. (on *Scorzonera* L.), *L. pusio* (Meig.) (on *Tragopogon* L.), *L. endiviae* Her. (on *Crepis* L.).

Napomyza aconitophila Hend. (on *Aconitum* L. and *Delphinium* L.), *N. rydeni* Her. (on *Ranunculus* L.).

Phytomyza fallaciosa Bri. (on *Ranunculus* L.), *Ph. anemones* Her. (on *Anemone nemorosa* L.), *Ph. hellebori* Kalt. (on *Helleborus* L.).

Phytomyza spondylii R. D. (on *Heracleum* L.), *Ph. pastinaceae* Hend. (on *Pastinaca* L.), *Ph. sii* Her. (on *Sium* L. and *Berula* Koch.) [Fig. 49—52].

Phytomyza chaerophylliana Her. (on *Chaerophyllum* L.), *Ph. pimpinellae* Hend. (on *Pimpinella* L.).

Phytomyza lithospermi Nowak. (on *Lithospermum* L.), *Ph. pulmonariae* Nowak. (on *Pulmonaria* L. and *Symphytum* L.), *Ph. symphyti* Hend. (on *Symphytum officinale* L.), *Ph. myosotica* Nowak. (on *Myosotis* L.).

Phytomyza petoei Her. (on *Mentha* L.) [Fig. 20], *Ph. scotina* Hend. (on *Salvia* L.).

Phytomyza obscura Hend. (on *Satureja* L. s. l.), *Ph. origani* Her. (on *Origanum* L.), *Ph. tetrasticha* Hend. (on *Mentha* L.).

Phytomyza lappina Gour. (on *Arctium* L.), *Ph. eupatorii* Hend. (on *Eupatorium* L.).

Phytomyza zonata Zeit. (on *Melampyrum nemorosum* L.), *Ph. tenella* Meij. (on *Eupharasia* L.), *Ph. pedicularis* Her. (on *Pedicularis* L.).

Phytomyza ranunculivora Her. (on *Ranunculus acer* L., *R. repens* L., etc.), *Ph. linguae* Lundq. (on *Ranunculus lingua* L. and R. *flammula* L.) [Fig. 47—48].

Phytomyza solidaginis Hend. (on *Solidago* L.), *Ph. erigerophila* Her. (on *Erigeron* L.).

Phytomyza tanaceti Hend. (on *Tanacetum* L.), *Ph. leucanthemi* Her. (on *Chrysanthemum* L.), *Ph. klimeschi* Her. (on *Achillea* L.) [Fig. 68—69].

The "biological" replacement (vicariation) of closely allied Agromyzid species occurring in common at least over Central and North Europe, including Great Britain (cf. Hering, 1957a) can hardly be recognized as an adequate proof of sympatric speciation, since we do not know accurately the areas of the geographical distribution of these species and since the areas of distribution of their host plants do not or did not originally coincide. We know, however, that the areas of distribution of the Agromyzid species are in many cases very wide and at the same time broken by geographic barriers, so that they may stretch over the whole Palaearctic Region together with its islands, e. g. from the Canary Isles, Great Britain and Iceland as far as the Japanese Islands, and even over the whole Holarctic Region (cf. Hendel, 1931—1936; Frick, 1952; Sasakawa, 1953—1958; Spencer, 1956; Hering, 1957a). It seems that these areas can sometimes cover those of the host plants. These facts bear witness that the individuality of the hosts plays a more important part than both the geographic barriers and climatic factors in the speciation of these dipterous insects, just as is the case with the species-formation of other host specialized parasites. This view is closely linked with the theory of correlated evolution of both hosts and parasites (cf. pp. 165—171).

It is generally agreed that in the speciation of both animals and plants ecological isolation is supplemented by geographical isolation since the two

factors scarcely act separately; in nature we usually observe many intermediate stages between the two, i. e. ecogeographical isolation. Similarly, biological (host) isolation being the chief factor in speciation of host specialized parasites cooperates with ecological isolation of other kinds as well as with geographical isolation. The more the areas of the host distribution and their ecological characters differ, the more efficient should this cooperation be. When hosts are geographic vicariants, the parasite species-formation under their influence is, at the same time, a geographic one. *Phytomyza angelicae kibunensis* SASAK. on *Angelica polyclada* FRANCH. and *A. kiusiana* MAXIM., for instance, or *Phytomyza senecionis ravasternopleuralis* SASAK. on *Senecio palmatus* FALL., both subspecies described by SASAKAWA from Japan (1953, 1955a), are replacing "biologically" as well as ecologically and geographically the Europaean nominal subspecies. After the genital apparatus of Nearctic species have been examined, their many-sided vicariation with regard to Palaearctic ones will no doubt be revealed too.

Since the so-called geographical speciation is nothing but a borderline case of the process of species-formation directed mainly by ecological isolation of various kinds, we believe that certain notions applied to geographic vicariants may also be applied to ecological vicariants and particularly to certain biological vicariants, namely closely related parasitic forms adapted to different hosts. In particular we suggest following HUXLEY (1942) the terms polytypic species (= Rassenkreis) and superspecies (= Artenkreis)[1] introduced by RENSCH and MAYR (cf. MAYR, 1942) to denote groups of closely related allopatric subspecies or species to be applied also with regard to corresponding sympatric species groups. The extension of the superspecies concept to groups of ecologically and biologically vicariant sibling species occuring together in wide geographical areas is considered useful for the simple reason that the extremely poor structural differentiation of these species is an obvious proof of their direct relationship but, at the same time, raises difficulties in distinguishing them from ecotypes and ecophenotypes. The superspecies though originating directly from polytypic species should not be recognized as a particular kind of species but merely as a monophyletic group of species of a low degree of divergency, i. e. an elementary genus. In certain cases it may reach the taxonomic rank of a subgenus or even that of a genus, depending on the individual evaluation of the investigator.

It must be stressed that occurence of various sympatric species of *Agromyzidae* on the same host plant results in most cases in some ecological convergence. Deviations from this are not actually so frequent as it might have seemed from the artificial system of the family and from the not always very carefully composed host plant lists of the particular species. When the male genitalia are examined a lack of direct relationship in spite of a similar external morpho-

[1] Called by HUXLEY (1942) "supraspecies".

logy and of a common host plant is usually revealed. To different natural genera should be included for instance: *Phytomyza obscurella* FALL. and *Ph. pubicornis* HEND. (on *Aegopodium* L.), *Ph. hendeli* HER. and *Ph. albimargo* HER. (on *Anemone nemorosa* L.), *Ph. rectae pulsatillae* HER. and *Ph. campanariae* NOWAK. (on *Pulsatilla* MILL.), *Ph. tetrasticha* HEND. and *Ph. petoei* HER. (on *Mentha* L.), *Ph. ranunculi* (SCHRK.) and *Ph. fallaciosa* BRI. (on *Ranunculus* L.); to different subgenera or superspecies at least — the following: *Phytomyza matricariae* HEND. and *Ph. klimeschi* HER. (on *Achillea* L.), *Ph. aconiti* HEND. and *Ph. aconitella* HEND. (on *Aconitum* L. and *Delphinium* L.), *Ph. angelicae* KALT. and *Ph. angelicastri* HER. (on *Angelica* L.), *Ph. spondylii* R. D. and *Ph. heracleana* HER. (on *Heracleum* L.), *Ph. pauliloewi* HEND. and *Ph. pimpinellae* HEND. as well as *Ph. adjuncta* HER. and *Ph. melana* HEND. (on *Pimpinella* L.). Possession of a common host plant by some closely related Agromyzid species usually means secondary or accidental oligophagy, if it is not due to misidentification of either plants or insects. E. g. the alleged appearance of *Liriomyza pusio* (MEIG.) on *Scorzonera* L. (together with *L. scorzonerae* RYD.), of *Phytomyza obscura* HEND. on *Mentha* L. (together with *Ph. tetrasticha* HEND.), of *Ph. tetrasticha* HEND. on *Satureja* L. (together with *Ph. obscura* HEND.), of *Ph. myosotica* NOWAK. on *Symphytum* L. (together with *Ph. symphyti* HEND.) should be explained rather by misidentification. A number of other similar cases should be checked, e. g. the occurrence of *Phytomyza ramosa* HEND. on *Succisa* NECK. (together with *Ph. olgae* HER.) and of *Ph. olgae* HER. on *Knautia* L. (together with *Ph. ramosa* HEND.). On the other hand, the occurrence of *Amauromyza lamii* (KALT.) on *Ballota* L. [together with *A. morionella* (ZETT.)], and of *A. morionella* (ZETT.) on *Lamium* L. [together with *A. lamii* (KALT.)], of *Calycomyza humeralis* (ROS.) on *Solidago* L. [together with *C. solidaginis* (KALT.)], of *Liriomyza sonchi* HEND. on *Hieracium* L. [together with *L. pusilla* (MEIG.)], of *Phytomyza spondylii* R. D. on *Pastinaca* L. (together with *Ph. pastinacae* HEND.) are most likely the result of a secondary expansion from the primary host plant to a related plant which has thus become a secondary (accessory) host plant. The secondary character of the oligophagy is seen here from the fact that the related Agromyzid species occuring on the same plant differ, at the same time, clearly in their choice of the primary (main) host plant. This is quite an analogous phenomenon to that observed with former geographic vicariants, the distribution areas of which overlap as a result of a secondary territorial expansion. Closely related host plants can be compared to islands of an archipelago on which animal species originated and migrated afterwards to other islands in the vicinity. Most cases of common occurrence of closely related Agromyzid species on the same host plant have been recorded among parasites of the *Gramineae* and *Carex* L. (the group of *Agromyza ambigua* FALL., of *A. cinerascens* MACQ., *Cerodontha* ROND. and *Metopomyza* ENDERL.). This may be explained by the considerable resemblance of the leaves of the grasses as well as the resemblance

of the mines produced in them. These two kinds of resemblance seem to have given rise to both reshuffling of phytophagous fauna and misidentifications of plant and insect species. According to the material collected and examined by the author the shuffling in question is not so complete as would seem from the literature. Geographic speciation in its strictest sense, however, or an adaptation to various habitats (biotopes) might quite often have played a more important part here, than that of isolation under the influence of different host plants. This supposition could also be true in the comparatively few cases in which very closely related parasites of Dicotyledons do not differ even in their choice of the primary host plants, e. g. *Phytagromyza populi* (Kalt.) and *Ph. populicola* (Hal.) (on *Populus nigra* L.), *Phytomyza obscurella* Fall. and *Ph. podagrariae* Her. (on *Aegopodium podagraria* L.), *Phytomyza calthophila* Her. and *Ph. calthivora* Hend. (on *Caltha palustris* L.). It should be noticed that the sister species mentioned as living on the common host plants differ mainly in the degree of their advance in the directional evolution of the larval spiracles (cf. p. 131). The three sibling species treated as races of *Liriomyza* (*Cephalomyza*) *cepae* (Her.) feeding on *Allium* L. are differentiated in the same way. Hering (1956b) considered these forms to have been brought independently to Germany, thus they seem to be geographical vicariants (cf. Hering, 1957b).

In certain cases the adaptation of feeding habits to various plant organs and tissues was taken to have been the motor of speciation. Hering (1949) has described biological subspecies of *Phytomyza ranunculi* (Schrk.) differing mainly as to the place and manner of feeding, and later (1958a) certain species of *Phytomyza* Fall. living in various stem tissues of *Clematis recta* L. We cannot comment, however, on these examples, since we do not know the genital apparatus of the forms in question. Such "conjuncted species" are known in parasitology but among the *Agromyzidae* they seem to occur rather seldom. Adaptation to various plant tissues and organs must have been here linked in most cases with that to various plant species or groups. For instance, the species of *Phytomyza* Fall. living in seed capsules of *Melampyrum* L., *Eupharasia* L. and *Pedicularis* L. and species mining in the leaves of *Veronica* L., and *Digitalis* L. belong together to one natural genus.

Retarded Evolution

The relation between phytophagous insects and their host plants has been formed as a result of the evolution of the two partners. Some preponderance of systematic oligophagy on the level of the species and that of the genus as well as preponderance of biological replacement can be partly explained by means of the theory of correlated evolution of hosts and parasites. The theory has been included in the parasitogenic rules, i. e., parasitological correlation rules (parasitologische Korrelationsregeln), which we shall try to verify as

applied to the discussed group of parasites of plants. We quote these rules as formulated by Eichler (1942):

1) Fahrenholz' rule. "Bei zahlreichen (vorwiegend ständigen) Parasiten ist mit der historischen Entwicklung und Aufspaltung der Wirte gleichlaufend auch eine entsprechende Entwicklung und Aufspaltung der Parasiten einhergegangen. Aus den sich ergebenden verwandtschaftlichen Beziehungen der Parasiten lassen sich deshalb Rückschlüsse ziehen auf die (oft verdeckten) Verwandtschaftsverhältnisse der Wirte".

Fahrenholz' rule has also been referred to as the rule of the parallel evolution (Stammer, 1957) or that of phylogenetic parallelism (cf. Eichler, 1940). In order, however, not to confuse parallel evolution of hosts and parasites with phylogenetic parallelism of related parasitic groups (cf. pp. 114—133), the former will be referred to as correlated evolution.

Since Fahrenholz' rule has sometimes been interpreted as that of simultaneous speciation of hosts and parasites, the conception of retarded evolution of parasites (Hopkins, 1942; cf. Szidat, 1956) is considered to be a certain modification of the above. According to this concept the evolution and speciation of parasites have always been lagging behind and following those of their hosts. The changes of the host must go beyond a certain limit, before the parasite changes take place. That is why on higher taxonomic units of hosts live lower taxonomic units of parasites, e. g. a parasitic species on a host genus, a parasitic genus on a host family and so on.

It is well known that animal evolution followed that of plants, wherever a closer link between an animal and a plant group had been established, particularly a symbiotic relation (in a broader sense, cf. Allee, 1949). A number of interested investigators (e. g. Petersen, 1930; Brues, 1946; Hering, 1951a; Painter, 1953) maintain that correlated evolution (referred to as "parallel evolution", and usually understood as retarded evolution) explains best the "botanical sense" of many phytophagous insects and certain perallels in the system of various insect groups and their host plants; they also hold, however, that in addition to correlated evolution occasional leaps of insects to plants, either related or even unrelated to their primary (original) hosts, have taken place.

The *Agromyzidae* are considered to be a phylogenetically young group, considerably retarded in their evolution and well behind that of the Angiosperms. The majority of the flies occur on the highest families of Angiosperms, such as *Compositae*, *Labiatae*, *Umbelliferae*, *Leguminosae*, *Gramineae* and *Cyperaceae*. From among the older families only the *Ranunculaceae* are frequently invaded. Agromyzids feed mainly on herbaceous plants which evolved secondarily from arboreous plants, while from among the xylophytes they choose almost exclusively those with deciduous leaves, which have been secondarily derived from xylophytes with winter-durable leaves (evergreen plants). The division of the family into few but large genera, comprising numerous and poorly differentiated species, has been also considered as an evi-

dence of its late origin (FRICK, 1952). Although a more profound study of the morphology of the adults will show that neither are the genera so large nor the species so poorly differentiated, as has been believed up till now, the fairly frequent occurrence of sibling species, particularly in apomorphous groups, speaks in favour of the phylogenetic youth of the family and its ability to continue its specializing evolution.

The natural system of the *Agromyzidae* which is now emerging as a result of the examination of their genital apparatus reveals a number of links with that of the Angiosperms (cf. pp. 96—107, 154). However, clear parallels between the two systems are to be found merely on the level of lower taxonomic units, and give way as higher and higher units are compared. Superspecies, subgenera and many genera of mining flies have usually been linked with groups of related genera, tribes, subfamilies, families and orders of plants. And yet related natural genera of the flies occur usually on unrelated plant groups, and the division of the family *Agromyzidae* into two subfamilies has nothing in common with any division of the Angiosperms. The degree of divergency of parasitic species belonging to the same subgenus corresponds sometimes to that of divergency of their host plant genera [cf. fig. 70]. The picture is more complex when parasites belonging to the same genus do not bear the same relation to each other as do their host plants and when host ranges of various subgenera of the same genus overlap (cf. pp. 163—165). Certain Angiosperm groups have been completely omitted by Agromyzids. The facts as well as the existence of various kinds of "phagism" on the level of species and genus (cf. pp. 134—138, 154) point to the late origin of the Agromyzids as compared to that of the Angiosperms and to a gradual expansion of the former to their host plants.

According to the opinion of dipterologists (cf. LINDNER, 1949; HENDEL, 1931; FRICK, 1952), the *Agromyzidae* could not have arisen until the upper Cretaceous, i. e. at the beginning of the Caenophytic era when the Angiosperms have already undergone their main radiations and spread over all continents, gaining preponderance in the world flora. Already in the upper Cretaceous there existed prototypes of many present genera of the Angiosperms. The *Agromyzidae* are to such degree adapted both biotically and structuraly to their endophytophagous habits that they seem to have arisen already after their ancestors abandoned saprophagy. There is only some very slight probability that a polyphagous species occuring on many unrelated plant groups found in the initial center of its origin has been an ancestor of the family. The ancestor must have been rather a limited oligophagous species attached to one plant family or even a monophagous species linked with the prototype of one plant genus; all the other host plant genera of the Agromyzids have been invaded by its offsprings through successive ecological expansions combined with territorial expansions. This could justify both a complete lack of Agromyzids on certain Angiosperm groups as well as wide disjunctions in host ranges. The present flourishing

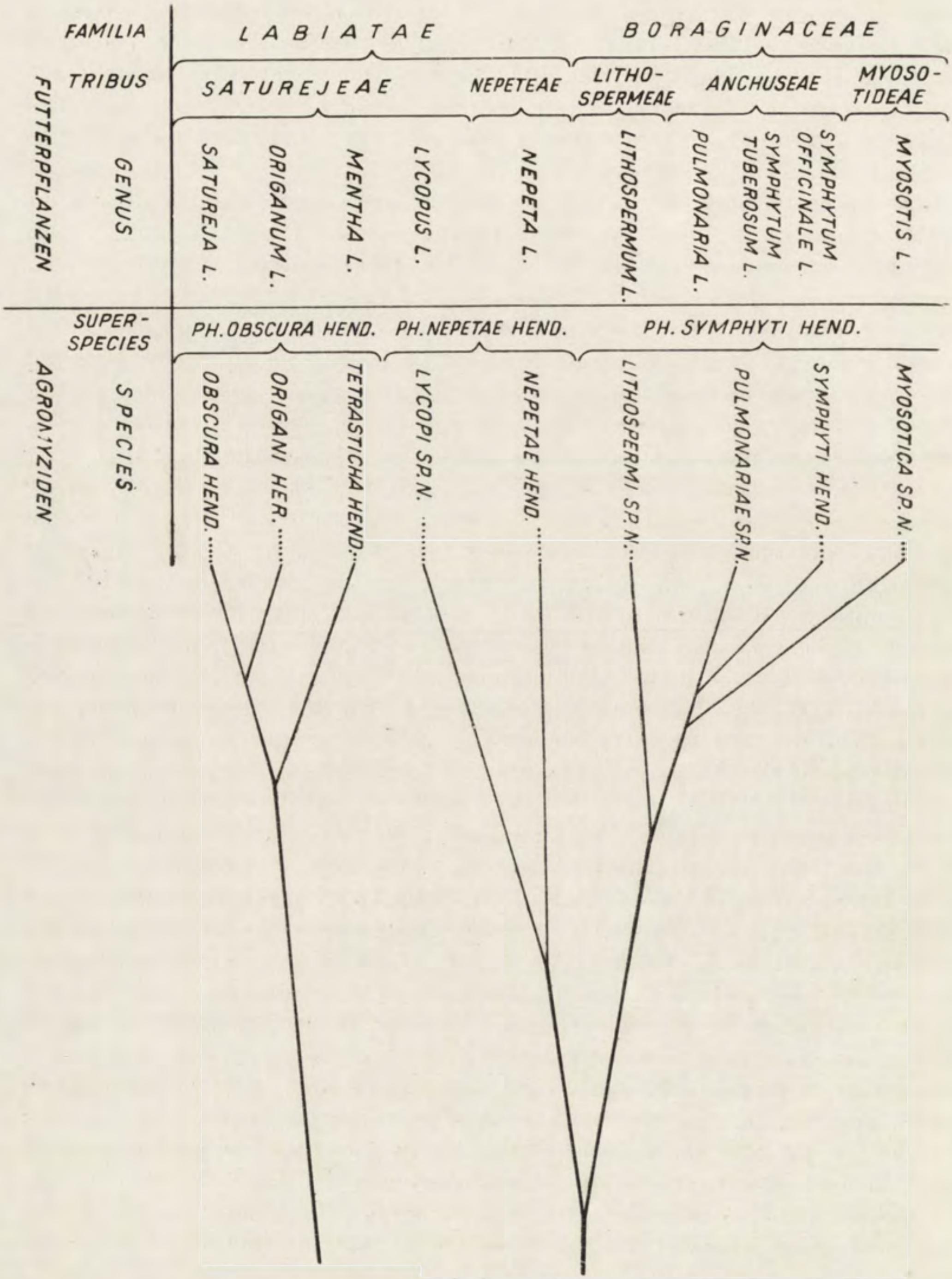


Fig. 70. Relationships within the former group of *Phytomyza obscura* HEND. as compared with the system of its host plants (after NOWAKOWSKI, 1959).

of the family and its extension over all continents and zones could not have begun earlier than in the Tertiary when large numbers of arboreous plants changed into herbaceous — the process lasting to the Quartenary. The few fossil remains of *Agromyzidae* are known from the Baltic amber of lower Oligocene age. The Pliocene and Pleistocene are taken as periods of great expansion and differentiation of the herbaceous plant genera (Stebbins, 1950). Hendel (1931) and Frick (1952) consider Europe to be the center of expansion of *Phytomyza* Fall. comprising the majority of apomorphous groups of the subfamily *Phytomyzinae*. Europe is also characterized by an overwhelming majority of herbaceous plants, as the Glacial period destroyed the largest percentage of arboreous plants on that continent.

The evolution of the *Agromyzidae* might have been retarded as it followed that of the plants, though, at the same time, it might have been faster in its tempo. One speciation of the host plants had to correspond to several speciations of the Agromyzids, since the new Agromyzid species originated as a result of the extension of earlier species to the already formed plant groups, various Agromyzid species settling independently on the same plant group and then diverging together with it but far quicker in their tendency to shift to monophagy.

The related, though "catching up" evolution of these parasites along with their leaps to secondary hosts, either related or unrelated with the primary (original) ones, justifies not merely a lack of parallels in the systems of two groups of organisms on the level of higher taxonomic units but also conspicuous deviations from it at the level of lower units. If parasite species-formations are considerably retarded as compared to those of their hosts, they may also not be strictly adjusted to them. For some reasons or other (cf. pp. 141—148) a parasite may omit some plant species or, on the other hand, may choose some other though directly unrelated but more alike in other respects, e. g. in geographic distribution, ecological character or morphological and phytochemical features of the invaded organs. Since there are leaps to related plants, systematic oligophagy does not always correspond to the so-called phylogenetic host specificity.

The mutual verification of the host and parasite systems must thus be based on a many-sided knowledge of both these groups of organisms. The occurrence of the same or closely related phytophagous insect species on some plants does not prove the relationship between these plants to be a direct one, but rather unables us to expect such a relationship or an affinity of some other kind.

2) Szidat's rule: "Die Neigung zur Höherentwicklung der Wirte färbt vielfach ab auf deren (vorwiegend ständige) Parasiten, so dass innerhalb vergleichbarer grosser Einheiten den Wirtsgruppen mit relativ niederer Organisationshöhe (primitivere Wirte) auch Parasiten mit relativ niederer Organisationshöhe (primitivere Parasiten) zu eigen sind".

When the Agromyzids appeared on the stage, all or nearly all Angiosperm families had already been there, and thus they did not have to conquer plesiomorphous plant families earlier than apomorphous ones. Thus, the plesiomorphous representatives of this dipterous group could live on plant families at various levels of apomorphy. When, however, trying to choose the forms less distant from the common ancestor, the evolution of host specificity must be taken into consideration together with that of topospecificity.

Thus, it is of great importance to clear up the ecology of *Encoelocera bicolor* LOEW, a species which in many respects (large body size, structure of the forehead, wing venation, abundant bristles, primitive, symmetric genital apparatus) could pretend to be taken for the most plesiomorphous from among the recent Agromyzids.

The genus *Phytobia* LIOY (= *Dendromyza* HEND.) living in the cambium of xylophytes belonging to the plesiomorphous families *Betulaceae*, *Salicaceae* and *Rosaceae*, seems to be distinctly plesiomorphous too. If it is to be considered as the ancestor of other *Agromyzidae*, the assumption must be made that these dipterous insects fed originally in the cambium of some primitive arboreous Angiosperms and it was not until later that they passed over to herbaceous ones. The forms mining leaves of xylophytes are, however, of a secondary descent from various forms mining leaves of herbs.

Recently HERING (1957c), however, has recognized the feeding in liver mosses to be original. *Liriomyza mesnili* D'AGUILAR and *L.* spec. from *Megaceros* CAMPBELL belong according to their adult characters to the subfamily *Phytomyzinae*, and according to their larval features they could be included in the subfamily *Agromyzinae*, and as such they seems to be close to the common ancestor of the two subfamilies. Larvae or mines on liver mosses are known from Europe, the West Indies, from Juan Fernandez and New Zeeland. In consequence of HERING's view, an assumption could be made that the origin of the *Agromyzidae* consisted in shifting from saprophagy to feeding in the thallus of liver mosses, and that vascular plants have been conquered as a result of a secondary expansion. In case this hypothesis were correct, SZIDAT's rule would be of wider application here.

3) EICHLERS's rule: "Unter in sich gleichwertigen, grösseren systematischen Einheiten von Wirten haben diejenigen Gruppen, welche eine reiche Gliederung aufweisen, auch eine grössere Mannigfaltigkeit des (vorwiegend Ständigen) Parasitenbestandes, als diejenigen mit geringer Gliederung".

As an overwhelming majority of Agromyzids live on the highest families of Angiosperms (cf. p. 166), this fact might show the flourishing periods of the plant families to coincide with those of their parasites. The highest Angiosperm families have also the largest numbers of their representatives, and thus, EICHLER's rule can be applied, as far at least as the better examined European fauna of the *Agromyzidae* is concerned. From among the older plant families more differentiated and richer in species, *Ranunculaceae* alone

have an abundant Agromyzid fauna. There are merely single oligophagous species that live on the *Caryophyllaceae*, *Cruciferae* and *Rosaceae*. Small and poorly differentiated Angiosperm families nourish usually also still poorer faunas of mining flies.

* * *

In these "Remarks on Host Plant Selection by Mining Flies" a number of facts has been gathered and a number of problems has been touched upon in trying to grasp the relation of these phytophagous insects to their host plants from an evolutionary point of view. We hope that elaboration and solution of the problems will be provided by further, more detailed taxonomic and ecological studies, as well as by physiological and genetic investigations.

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STRESZCZENIE

W części wstępnej „O trzech zasadniczych cechach systematyki neontologicznej" autor określił systematykę biologiczną jako naukę o naturalnym układzie organizmów, a układ naturalny jako układ konsekwentnie filogenetyczny. Wykazał on, że systematyka neontologiczna jest:

1) filogenetyczna, ponieważ traktuje gatunki jako etapy i stany równowagi procesu ewolucyjnego i ponieważ klasyfikuje je w układ hierarchiczny (w grupy monofiletyczne) według kryterium pokrewieństwa filogenetycznego, czyli wspólnego pochodzenia, a przez to przyczynia się do rekonstrukcji drzewa rodowego organizmów,

2) obiektywna, ponieważ wyróżnia istniejące realnie w przyrodzie wspólnoty rozrodcze organizmów (gatunki) i ponieważ łączy gatunki w grupy monofiletyczne według obiektywnego kryterium pokrewieństwa filogenetycznego, uchwytnego w czasie,

3) wielostronna (kompleksowa), ponieważ rozróżnia wspólnoty rozrodcze organizmów i poznaje stosunki pokrewieństwa tych wspólnot za pomocą metody wzajemnego wyświetlania, opartej na analizie wszelkich podobieństw i różnic między organizmami.

We „Wstępie do rewizji systematycznej rodziny *Agromyzidae*" autor wykazał, że systematyka owadów minujących może opierać się na znajomości nisz ekologicznych i cyklów rozwojowych oraz na stałej konfrontacji danych ekologicznych z morfologicznymi i że może ona stosować metody i reguły parazytologiczne. Następnie przeprowadził autor krytykę obecnego stanu badań systematycznych nad omawianą grupą, których słabym punktem była powierzchowna znajomość morfologii postaci dorosłych, oraz uzasadnił potrzebę szczegółowej rewizji rodziny w oparciu o aparaty genitalne.

W rozdziale „Znaczenie pewnych aspektów badawczych” autor dokonał analizy wartości taksonomicznej zewnętrznej morfologii imago, aparatu genitalnego samca, oraz znaczenia larwy i miny. Stwierdził on, że trudność uprawiania systematyki *Agromyzidae* jedynie w oparciu o zewnętrzną morfologię imagines spowodowana jest z jednej strony nieuchwytnością różnic zewnętrznych między licznymi w tej grupie gatunkami bliźniaczymi (sibling species), a często nawet między gatunkami bliżej niespokrewnionymi, które określił jako “pseudo-sibling species”, z drugiej zaś szeroką skalą zmienności wewnątrzpopulacyjnej. Autor rozpatrzył przy tym krytycznie znane przypadki polimorfizmu (polichromatyzmu) i zarejestrował parę nowych przykładów.

Autor wykazał, że aparat genitalny samca, dotychczas prawie wcale nie wykorzystywany przez systematykę *Agromyzidae*, ma wysoki walor taksonomiczny z powodu swego silnego zróżnicowania w obrębie grupy przy stosunkowo słabej zmienności wewnątrzpopulacyjnej; na walor ten wskazuje wysoki stopień korelacji cech genitalnych z cechami niszowymi. Ta specyficzność, której nie można wytłumaczyć samą komplikacją budowy genitaliów, przemawia za istnieniem izolacji mechanicznej, pojmowanej jednak tylko w sensie negatywnego czynnika doboru płciowego. Autor z jednej strony podał szereg przykładów łatwego rozróżniania gatunków z trudnych grup przez porównanie aparatu genitalnego, z drugiej zaś wykazał tą drogą konspecyficzność kilku form opisanych na podstawie morfologii zewnętrznej. Z powodu komplikacji budowy genitaliów przy silnym ich zróżnicowaniu w obrębie grupy, znajomość tych aparatów jest konieczna przy ustalaniu naturalnych pokrewieństw gatunków. Autor wykazał, że klasyfikacja oparta również na aparatach genitalnych wymagałaby rozbicia nielicznych wielkich rodzajów sztucznych na liczniejsze i na ogół mniejsze rodzaje naturalne, będące często grupami wikariantów biotycznych, żerujących na spokrewnionych roślinach żywicielskich. Dokonując częściowej rewizji podrodziny *Phytomyzinae*, wyróżnił on liczne naturalne grupy gatunków i wyznaczył gatunki typowe trzech nowych rodzajów.

Pogłębienie znajomości morfologii imagines wykazuje powiązanie procesów dywergencji we wszystkich stadiach cyklu rozwojowego, pozorność poikilogonii oraz inkongruencji. Na skutek kierunkowości i równoległości ewolucji najbardziej plastycznych narządów larwalnych (spirakulów), budowa larw jest mniej zróżnicowana w obrębie grupy i mniej specyficzna od budowy aparatów genitalnych. U pięciu gatunków autor wykrył cyklomorfizm (dymorfizm sezonowy) larw.

Autor zwrócił uwagę, że oznaczanie gatunków owadów minujących według roślin żywicielskich i min polega na stosowaniu metody rozróżniania pasożytów poprzez żywicieli i odwrotnie (host-parasite discrimination method). Wiele form wyróżnionych dawniej na podstawie min i roślin żywicielskich okazało się dobrymi gatunkami po dokładniejszym zbadaniu ich morfologii, co wskazuje na wysoki walor taksonomiczny cech biotycznych.

W rozdziale „Kierunki ewolucyjne” autor wykazał sztuczność i poziomy przebieg wielu obecnych podziałów taksonomicznych wyróżniających polifiletyczne „grupy stadialne” i „negatywne” zamiast grup monofiletycznych. Wyróżnił on i zbadał cztery kierunki równoległej ewolucji w obrębie omawianej rodziny, wykazując częściowo ich przystosowawczy charakter — związek z pasożytniczym trybem życia larw. Zmniejszanie się rozmiarów ciała w filogenezie autor sprowadził tu głównie do działania parazytologicznej reguły Harrisona; z procesem tym próbował związać redukcję i koncentrację kostalną użyłkowania skrzydła (związaną również z mechaniką lotu) oraz redukcję oszczecenia. Rozrost i rozgałęzianie się spirakulów larw oraz zwiększanie się liczby otworków oddechowych jest usprawnieniem tych części aparatu oddechowego w warunkach endofagizmu, a niekiedy też przystosowaniem się ich do funkcji czepnej. Autor zwrócił uwagę, że równoległa ortoewolucja w obrębie grupy nie zawsze wiąże się ze specjacją dywergencyjną, że zaznaczają się pewne przekrzyżowania tych dwu dróg ewolucji.

„Uwagi na temat wybiórczości *Agromyzidae*” rozpoczynają się rozdziałem „Specyficzność roślin żywicielskich”, w którym autor stwierdził dominację wąskiego oligofagizmu systematycznego zarówno nad monofagizmem ścisłym, jak i nad oligofagizmem systematycznym wyższych stopni, oligofagizmem dyzjunktywnym oraz polifagizmem. Uznając pewną płynność granic między oligofagizmem a ksenofagizmem (w szerszym znaczeniu) autor podał w wątpliwość przytaczane w piśmiennictwie przykłady ksenofagizmu (w węższym znaczeniu).

W rozdziale „Wpływ pewnych czynników na wybór rośliny żywicielskiej” autor starał się znaleźć przyczyny odchyleń od oligofagizmu systematycznego i wykazał, że na wybór rośliny przez fitofaga mogą mieć wpływ — oprócz specyficznych protein roślinnych — również „substancje atrakcyjne”, dalej rozmieszczenie geograficzne rośliny oraz cechy anatomiczne atakowanych narządów roślinnych, związane znów z formą wzrostową i typem ekologicznym rośliny. W związku ze swą czerwiowatą budową, hygrofilnością i cieniolubnością endofagiczne larwy muchówek unikają liści twardych (skórzastych), jak również liści zbyt drobnych (które nie dostarczyłyby im zresztą dostatecznej ilości pokarmu), przekładają hygrofity i mezofity nad kserofity, a rośliny zielne nad drzewiaste.

W rozdziale „Rozmieszczenie *Agromyzidae* na tle roślinności” autor starał się wykazać, że fauna tych muchówek zależy przede wszystkim od trofizmu siedliska (gleby), nie tylko dlatego, że roślinność siedlisk oligotroficznych jest uboga, lecz również dlatego, że przeważają w niej gatunki kseromorficzne. Poza tym środowiska wilgotne są dogodniejsze od suchych, zacienione od niezacienionych, podłoże nie zalane od zalanego wodą, roślinność zielna od drzewiastej. Zależności te autor zilustrował przez porównanie faun kilku zespołów leśnych niżu polskiego. Przy przejściu do zbiorowisk związanych z siedliskami oligotroficznymi stwierdził on gwałtowne zubożenie fauny spowodowane

wypadnięciem prawie wszystkich gatunków roślin żywicielskich. Głównie przewagą roślinności kseromorficznej autor próbował też wytłumaczyć ubóstwo fauny tajgi, tundry i strefy śródziemnomorskiej w porównaniu z fauną strefy lasów liściastych i mieszanych w Europie, jak również ubóstwo fauny strefy wysokogórskiej w porównaniu z fauną regla dolnego.

W rozdziale „Związek specjalizacji pokarmowej ze specjacją" autor wykazał, że w ewolucji w obrębie omawianej grupy dominuje zawężanie zakresu roślin żywicielskich, swoistych dla poszczególnych gatunków fitofagów, i dążenie do monofagizmu. Obok tego procesu ma jednak miejsce ekspansja na żywicieli wtórnych, spokrewnionych lub niespokrewnionych z pierwotnymi, prowadząca niekiedy nawet do polifagizmu. Rozległość, wielostrefowość i dyzjunktywność arealów wielu gatunków *Agromyzidae*, jak również występowanie gatunków bliźniaczych i w ogóle gatunków blisko spokrewnionych na tym samym obszarze geograficznym, lecz na różnych, i to zwykle na spokrewnionych roślinach żywicielskich, przemawia za istnieniem specjacji sympatrycznej zachodzącej poprzez „rasy biologiczne". Autor wykazał, że występowanie kilku gatunków sympatrycznych na tej samej roślinie żywicielskiej polega najczęściej na konwergencji ekologicznej.

W rozdziale „Ewolucja opóźniona" autor próbował sprawdzić reguły parazytogeniczne na omawianej grupie pasożytów roślin. Za tym, że *Agromyzidae* rozpoczęły swą ewolucję znacznie później niż rośliny okrytozalążkowe i stopniowo rozprzestrzeniały się na te rośliny, przemawia występowanie znacznej większości tych fitofagów na najwyższych rodzinach *Angiospermae* i na gatunkach zielnych, brak równoległości układów systematycznych żywicieli i pasożytów na szczeblach wyższych jednostek taksonomicznych oraz znaczne odchylenia od tej równoległości na szczeblach niższych jednostek, jak również pominięcie wielu grup *Angiospermae*. Ze względu na brak wspólnego rytmu specjacji żywicieli i pasożytów oraz przeskoki pasożytów na żywicieli wtórnych, spokrewnionych lub niespokrewnionych z pierwotnymi, „reguła ewolucji równoległej" Fahrenholza nie ma tu szerszego zastosowania. Bardzo ograniczony zasięg ma również reguła Szidata, jakkolwiek jest możliwe, że *Agromyzidae* żyły pierwotnie w kambium prymitywnych drzewiastych *Angiospermae* i dopiero wtórnie przerzuciły się na zielne okrytozalążkowe. Dość szerokie zastosowanie znajduje reguła Eichlera, ponieważ najwyższe rodziny *Angiospermae* są jednocześnie rodzinami reprezentowanymi przez największe liczby rodzajów i gatunków.

РЕЗЮМЕ

Во вступительной части „О трех основных чертах неонтологической систематики" автор определяет биологическую систематику как науку о естественной системе организмов, а естественную систему как систему последовательно филогенетическую. Он доказывает, что неонтологическая систематика является:

во-первых, филогенетической, так как рассматривает вид как этап, или состояние равновесия, в эволюционном процессе и группирует виды в иерархическую систему (в монофилетические группы), применяя критерий филогенетического родства, т. е. общего происхождения, и тем самым содействует реконструкции родословного древа организмов;

во-вторых, объективной, так как выделяет реально существующие в природе сообщества скрещивающихся организмов (т. е. виды) и объединяет виды в монофилетические группы, применяя критерий филогенетического родства, уловимого во времени;

в-третьих, многосторонней (комплексной), так как различает сообщества скрещивающихся организмов и обнаруживает родство этих сообществ, пользуясь методом взаимного разъяснения, основанным на анализе каждого сходства и каждого различия между организмами.

Во „Введении в систематическую ревизию семейства *Agromyzidae*" автор доказывает, что систематика минирующих насекомых может основываться на знании экологических ниш и циклов развития: она имеет возможность постоянно сличать морфологические данные с экологическими и может пользоваться паразитологическими методами и закономерностями. Далее автор подвергает критическому анализу методы и итоги систематических исследований рассматриваемой им группы; их слабой стороной является, по его мнению, поверхностное исследование морфологии взрослых особей, чем он и обосновывает необходимость детальной ревизии этого семейства, причем предлагает положить в ее основу прежде всего исследование гениталий.

В главе „Значение некоторых аспектов исследований" автор анализирует таксономическую пригодность внешней морфологии имаго и генитального аппарата самца, а также таксономическое значение личинки и мины. Он считает, что трудность построения системы семейства *Agromyzidae* на основании внешней морфологии взрослых особей заключается, с одной стороны, в неуловимости внешних различий между многочисленными в этой группе видами-двойниками (sibling species), а часто даже и между видами далеко не родственными, которые определены автором как виды-псевдодвойники (pseudo-sibling species); с другой стороны, — в широком масштабе внутрипопуляционной изменчивости. Автор обсуждает при этом уже известные случаи полиморфизма (полихроматизма) и регистрирует несколько новых примеров этого явления.

Автор утверждает, что генитальный аппарат самца, до сих пор почти совсем не использованный систематикой семейства *Agromyzidae*, представляет большую таксономическую ценность вследствие сильной его дифференцировки в пределах группы при относительно слабой внутрипопуляционной изменчивости; на важное его значение указывает высокая степень корреляции генитальных признаков с естественными биотическими признаками. Эта видовая специфика — которую нельзя объяснить одной только сложностью строения гениталий — может служить подтверждением наличия механической изоляции, понимаемой, однако, исключительно как отрицательный фактор полового отбора. Автор приводит, с одной стороны,

ряд примеров, показывающих, как легко можно различить виды из трудных групп, сравнивая генитальные аппараты имаго; с другой стороны, он таким образом выявляет видовую идентичность нескольких форм, ранее описанных только по внешним морфологическим признакам. Ввиду сложности строения гениталий при высокой степени их дифференцировки в пределах группы, исследование генитального аппарата является необходимым условием установления естетсвенного родства видов. Автор утверждает, что, проводя классификацию, опирающуюся также и на исследовании генитальных аппаратов, необходимо будет разбить малочисленные, искусственные, обширные роды на более многочисленные, естественные роды, в большинстве случаев более мелкие, которые часто являются группами биотически викарирующих видов, питающихся на родственных кормовых растениях. При частичной ревизии подсемейства *Phytomyzinae* автору удалось выделить целый ряд естетсвенных групп видов. При этом им были определены типовые виды трех новых родов.

При более детальном исследовании морфологии имаго обнаруживается связь между процессами дивергенции во всех стадиях цикла развития, а также мнимость поикилогонии и инконгруэнции. Ввиду направленной и параллельной эволюции наиболее пластических личиночных органов (спиракул), строение личинок оказывается менее дифференцированным в пределах группы и менее специфичным чем строение генитальных аппаратов. У пяти видов автор обнаружил цикломорфизм (сезонный диморфизм) личинок.

Автор отмечает, что при определении видов минирующих насекомых по кормовым растениям и минам применяется метод распознавания паразитов по их хозяевам и наоборот (host-parasite discrimination method). Более детальное исследование морфологии целого ряда форм, уже ранее выделенных на основании мин и кормовых растений, подтвердило принадлежность многих из них к числу действительно хороших видов, что также указывает на большое значение биотических признаков для таксономии.

В главе „Направления эволюции" выявляется искусственность и горизонтальный характер многих принятых в настоящее время таксономических делений, которые, по мнению автора, устанавливают полифилетические „стадиальные" и „отрицательные" группы, а не группы монофилетические. В пределах рассматриваемого семейства автор выделил и исследовал четыре направления параллельной эволюции, причем ему удалось отчасти выявить их адаптивный характер — связь с паразитическим образом жизни личинок. Уменьшение размеров тела в процессе филогенеза автор объясняет прежде всего действием паразитологического правила Harrison'a; он пытается связать с этим процессом редукцию и костальную концентрацию жилкования крыла (связанную, кроме того, с механикой полета), а также редукцию щетинок. Увеличение в объеме и разветвление спиракул личинок, а также умножение дыхательных пор, автор рассматривает как усовершенствование дыхательного аппарата в условиях эндофагизма, а иногда и как адаптацию его к прикрепительной функции. Автор отмечает, что параллельная ортоэволюция в пределах группы не всегда связана с дивергентным видообразо-

ванием и что до известной степени намечается как бы перекрещивание этих двух путей эволюции.

„Замечания по вопросу о выборе кормовых растений минирующими двукрылыми" начинаются главой „Специфика кормовых растений", в которой автор подчеркивает, что узкий систематический олигофагизм значительно преобладает как над строгим монофагизмом, так и над систематическим олигофагизмом высших степеней, над дизъюнктивным олигофагизмом и над полифагизмом. Допуская возможность перехода олигофагизма в ксенофагизм (в более широком смысле), автор сомневается в правильности приводимых в литературе примеров ксенофагизма (в более узком смысле).

В главе „Влияние некоторых факторов на выбор кормовых растений" автор, пытаясь раскрыть причины отклонений от систематического олигофагизма, приходит к выводу, что на выбор фитофагом кормового растения могут оказать влияние, кроме специфических растительных протеинов, также и „привлекающие вещества"; затем играет роль географическое распространение растения и анатомические черты подверженных нападению его органов, связанные в свою очередь с формой роста и экологическим типом растения. Эндофагические личинки двукрылых, червеобразные по своему строенню, гидрофильные и тенелюбивые, избегают твердых (кожистых) листьев, а также листьев слишком мелких (которые, впрочем, не могли бы предоставить им достаточного количества питания); они предпочитают гидрофиты и мезофиты ксерофитам и травянитые растения — деревянистым.

В главе „Распределение фауны *Agromyzidae* на растительности" автор пытается доказать, что фауна этих двукрылых зависит прежде всего от трофизма почвы: это вытекает не только из того, что растительность олиготрофических почв скудна, но также и из факта, что в ней преобладают ксероморфические виды. Кроме того, влажная среда более благоприятна, чем сухая, затененная лучше незатененной, субстрат не залитый водой обладает несомненными преимуществами перед субстратом залитым и травянистая растительность перед деревянистой. Эту разнородную зависимость автор иллюстрирует, используя сравнение фауны нескольких типов леса польской низменности. При переходе на растительные сообщества, связанные с олиготрофическими почвами, он констатирует резкое понижение численности видов и особей семейства *Agromyzidae*. Это явление объясняется, по его мнению, отсутствием почти всех видов кормовых растений. Бедность фауны тайги, тундры и Средиземноморья по сравнению с фауной зоны лиственных и смешанных лесов в Европе, а также бедность ее в высокогорной зоне по сравнению с нижней лесной зоной, тоже приписывается автором в первую очередь преобладанию ксероморфической растительности.

В главе „Связь пищевой специализации с видообразованием" автор доказывает, что в эволюции в пределах рассматриваемой им группы доминирует процесс сужения круга кормовых растений, специфичных для отдельных видов фитофагов, и стремление к монофагизму. Однако наряду с этим наблюдается и экспансия на вторичных хозяев, родственных или не родственных первоначальным, которая

иногда ведет к полифагизму. Обширность и трансзональный характер ареалов многих видов семейства *Agromyzidae*, часто встречающаяся в этих ареалах дизъюнкция, а также наличие видов-двойников и вообще видов близкородственных в одном и том же районе, хоть и на различных — обычно все же родственных — кормовых растениях, может служить подтверждением симпатрического образования видов из „биологических рас''. Автор доказывает, что питание нескольких симпатрических видов на одном и том же кормовом растении обычно является экологической конвергенцией.

В главе „Запоздалая эволюция'' автор обсуждает проявления паразитогенических закономерностей в пределах рассматриваемой им группы паразитов растений. Эволюция семейства *Agromyzidae* началась значительно позднее, чем эволюция покрытосемянных, которые впоследствии стали областью экспансии его видов. В пользу этого утверждения свидетельствуют следующие факты: значительное большинство этих фитофагов питается на наиболее высокоразвитых семействах покрытосемянных и на травянистых видах; на уровне высших таксономических единиц отсутствует параллелизм систем хозяев и паразитов, а на уровне низших наблюдаются значительные отклонения от него; кроме того, виды семейства *Agromyzidae* не встречаются на многих группах покрытосемянных. Ввиду несогласованности видообразовательного ритма у хозяев и паразитов и случаев перехода паразитов на вторичных хозяев, родственных или не родственных первоначальным, правило параллельной эволюции Fahrenholz'а не может быть здесь широко применимо. Весьма ограниченное применение имеет также и правило Szidat'а, хотя возможно, что *Agromyzidae* жили первоначально в камбии примитивных деревянивтых покрытосемянных и лишь впоследствии переселились на травянистые. Досольно широко применимо правило Eichler'а, так как наиболее высокоразвитые семейства покрытосемянных являются в то же время семействами наиболее богатыми по числу родов и видов.

SUPPLEMENTARY NOTE

As this "Introduction" was handed over to the editor on July 1, 1959, the author could not take into consideration the papers published after this date, especially the most recent papers of M. Sasakawa and K. A. Spencer.
